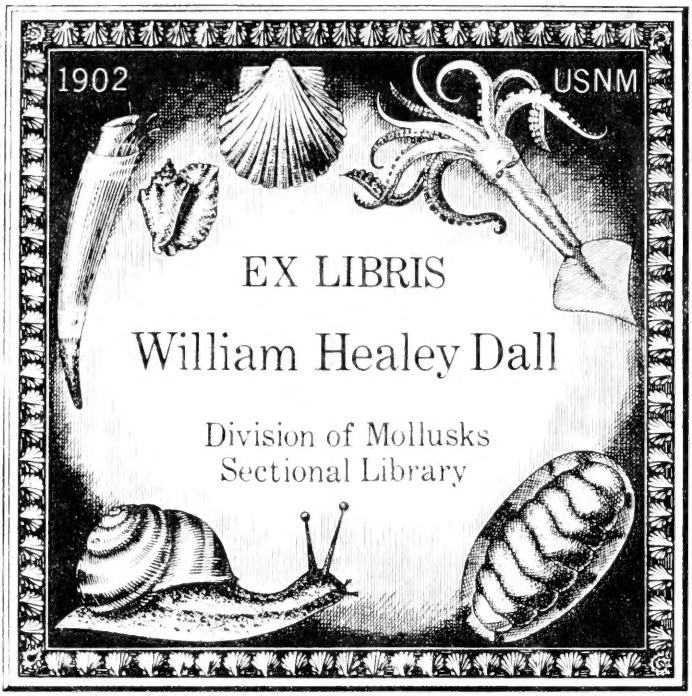

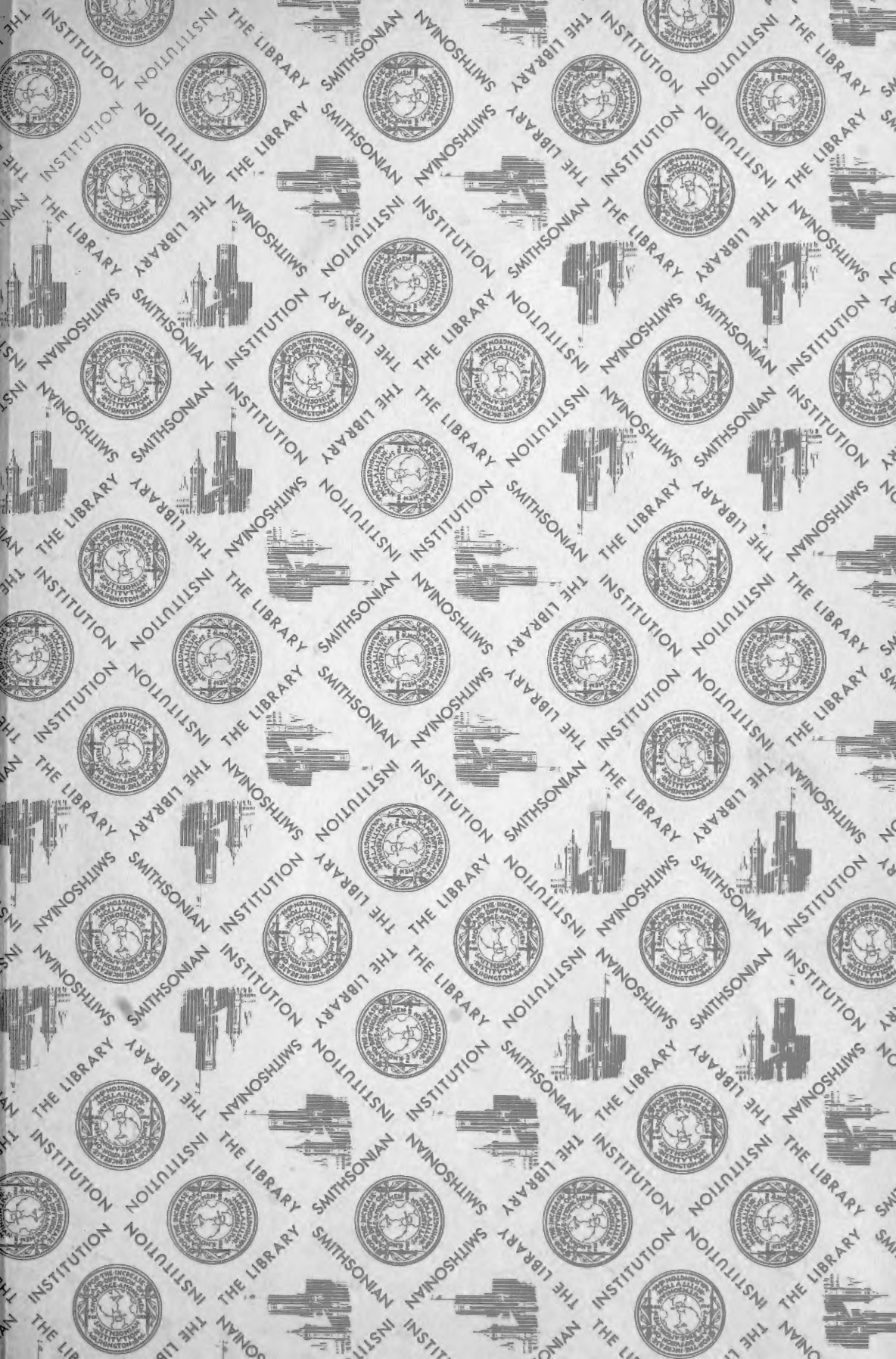
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THE CELL-LINEAGE AND EARLY LARVAL DEVELOPMENT OF FIONA MARINA, A NUDIBRANCH MOLLUSK.[1]

BY DANA BRACKENRIDGE CASTEEL, PH.D.

OUTLINE.

INTRODUCTION.

The study of the cleavage and early larval history of *Fiona marina* (Forsk.)[2] embodied in this paper was undertaken with the view of

[1] Contribution from the Zoölogical Laboratory of the University of Pennsylvania.

[2] Dr. H. A. Pilsbry, of the Academy of Natural Sciences of Philadelphia, has kindly assisted me in identification.

obtaining, as far as possible, an exact knowledge of the development of this Opisthobranch, in order that certain doubtful points regarding the embryology of Mollusks in general, and this group in particular, might be better understood. *Fiona* has proved in many ways a difficult object for study, but in certain respects offers advantages to the investigator. The exact origin of the germ layers as they arise in the segmenting egg has been particularly sought throughout the cleavage history, while in later stages attention has been directed to the rise of larval organs from their particular protoblasts where these could be definitely determined. Where this has been found impossible, approximate results are given. Certain questions have presented themselves both at the beginning and during the progress of this work, some of which may here be indicated briefly. Though it has not been my purpose to consider particularly the mechanics of cleavage, this phase of development has been borne in mind, and in certain instances discussed. Comparisons are made between the nearly equal cleavage of *Fiona* and the more unequal segmentation of many other molluscan and annelidan eggs. The manner of origin of the germ layers is naturally a point of cardinal interest to the cell-lineage worker, since by this method of investigation the most exact results are possible and very definite comparisons with other forms may be made. The exact derivation of the middle germ layer has been sought particularly. Has it a single or double mode of origin? If both "primary" and "secondary" mesoderm be present, which is "larval" and which forms permanent organs? How is the mesoderm segregated from the two primary germ layers? In the study of larval structure and development the excretory organs are of much interest, since widely diverse views are held regarding the mode of origin and the significance of both primitive and definitive molluscan kidneys. The axial relations between ovum and larva and the relations of the early cleavage planes to the median plane of the larva and adult are points of great interest. How and when does bilaterality first appear? When does trosion first become manifest and what is its immediate cause? These and other questions have arisen and have been borne in mind during the progress of the work. Unfortunately material for the study of later larval stages and metamorphosis has not been obtainable, so that a complete record of development from ovum to adult has been impossible.

The work was begun in the early summer of 1901, at the Zoölogical Laboratory of the University of Pennsylvania, and continued, together with general graduate study, during the two following years at this

University, as well as throughout the two intervening summers at the Woods Hole Marine Biological Laboratory.

I am glad to acknowledge the many courtesies extended to me at both institutions. I am particularly indebted to Prof. Conklin, at whose suggestion the work was undertaken, and it is a pleasure to express here my sincere appreciation of the valuable assistance which he has given me by way of suggestion and kindly criticism.

Material and Methods.

For the material upon which this study has been made, I am indebted to Drs. E. G. Conklin and M. A. Bigelow, by whom it was collected at Woods Hole, Massachusetts, during the summers of 1897 and 1898. The Nudibranchs were found spawning upon floating gulf-weed in Vineyard Sound, taken to the Laboratory and kept in aquaria for some weeks, where they spawned prolifically and where, from day to day, the eggs were collected and preserved. They were fixed in Kleinenberg's stronger picro-sulphuric solution and Boveri's picro-acetic for one-half to three-quarters of an hour and washed in 50 and 70 per cent. alcohol, as is the usual custom. Living material upon which to study the breeding habits of the animals has not been accessible to me, though search has been made in the same locality during the last two summers. This lack of the living adult animals and embryonic stages has been a considerable drawback, as it is particularly desirable that one investigating the developmental history of an organism should be able to observe its physiological activities and thereby verify conclusions gained through purely morphological work. The material at hand has been amply sufficient for carrying the work up to the stage of the free-swimming veliger, but not to the metamorphosis. It is my hope that in the near future material for the study of later stages and of the metamorphosis into the adult may be obtained, as many questions relative to the fate of larval organs must remain unanswered until this be accomplished.

Contrary to the conditions found among some other Nudibranchs, the gelatinous mass surrounding the egg-capsules does not become greatly hardened upon fixing, for upon being brought into water the jelly usually dissolves, leaving the eggs free in their individual capsules. The eggs may be sectioned without removing the jelly, as it cuts without difficulty. Both whole mounts and sections were stained in Delafield's hæmatoxylin diluted with six to ten times its volume of distilled water and slightly acidulated by the addition of a trace of HCl, or Kleinenberg's stronger solution after the method of Conklin.

This stain gives a reddish tint which differentiates the nuclei with great distinctness. Iron hæmatoxylin proved entirely unsatisfactory for sections of both early and late stages, for even in the old veligers almost all the cells are found to contain small yolk spherules which take up the hæmatoxylin so strongly and hold it so tenaciously that nuclei and cell walls are indistinguishable. Eggs which have just been stained and mounted are not favorable objects for study, but they should, if possible, stand for some time, the longer the better, until they gradually become more transparent by the penetration of balsam. Indeed, the most favorable slides are a few put up at the time the material was collected. By the addition of a little cedar oil to the balsam, or by moistening the edges of the cover with xylol at the time of using, it is always possible to roll the eggs by moving the cover—a very necessary process in cell-lineage work. Most of the observation and drawing was done with the aid of a Leitz objective 7, ocular 4, a Zeiss camera being used, with the paper at table level and plates reduced as indicated. A $\frac{1}{12}$ Leitz immersion was also used for observation when necsseary.

Nomenclature.

As a matter of convenience and for the sake of uniformity, I have followed the system used by Conklin (1897) with but slight variation.

A cleavage is oblique to the right when the upper daughter cell lies to the right of an imaginary observer whose body corresponds in position to the primary egg axis, his head being at the animal pole and facing the cell considered; *vice versa*, a division oblique to the left is one in which the upper cell lies to the observer's left. In the first instance the cleavage is *dexiotropic*, in the second *læotropic* (Lillie, 1895).

The term "quartet" is used to designate a generation of cells or their derivatives given off from the four cells meeting in the center of the vegetative pole, regardless of their fate. The different quartets are designated by coefficients placed before the letter indicating in which of the four quadrants the cells lie, while the cell generations are marked by exponents which follow the letter. The upper cell resulting from a cleavage is, in all cases, indicated by the smaller exponent; thus, $2b^{11}$ indicates the upper cell in B quadrant of the second quartet arising from the division of $2b^{1}$, while $2b^{12}$ is the lower. When the spindle lies in a horizontal direction or, in other words, when the cleavage plane is meridional, the cell which lies to the right is given the smaller exponent, to the left the larger. The capital letters A, B, C, and D are reserved for the four cells which meet at the center of the

vegetative pole ("macromeres") and from which the "micromeres" arise; for these latter the small letters a, b, c and d are used. Child (1900) and Treadwell (1901) have been followed in giving coefficients to the macromeres also, to indicate their generation, this being desirable when dealing with an egg in which, after the first few cleavages, the "macromeres" are large in name only. "Thus A, B, C, and D form the four-cell stage. At their next division from A arises 1A and 1a; from B, 1B and 1b, etc.; 1A then divides into 2A and 2a, while 1a divides into $1a^1$ and $1a^2$" (Treadwell).

Earlier Work on Opisthobranch Development.

A rather large number of older investigators have worked upon Nudibranch larval development. Grant (1827) described the veligers of *Æolis* and *Doris*. In 1837 Sars discovered that the young of *Tritonia, Doris* and *Æolis* possess a nautiloid shell; additional researches by the same investigator appeared in 1840 and 1845. Lovén (1839) described a number of Nudibranch larvæ together with those of other mollusks. Alder and Hancock's magnificent monograph upon the British Nudibranchs appeared in 1845 and contains a good general account of the results thus far obtained upon the subject of Nudibranch embryology. Reid in 1846 published an interesting paper upon the breeding habits of *Doris, Goniodoris, Polycera, Dendronotus, Doto*, etc., together with the constitution of the larvæ. An account of the embryology of *Tergipes* by Nordman appeared in the same year. An extremely thorough account of the development of the Tectibranch *Actæon* by Vogt also appeared in 1846. In 1848 Koren and Danielssen described the early stages of a number of Nudibranchs from the Norwegian coast. Schneider (1858) described the veliger of *Phyllorhöe*. Keferstein and Ehlers (1861) gave an account of some of the developmental stages of *Æolis*.

The later investigations of Langerhans (1873), Lankester (1875), Trinchese (1880–1–7), Lacaze-Duthiers and Pruot (1887), Rho (1888), Mazzarelli (1892–3–5), Heymons (1893), Viguier (1898), Carazzi (1900), Guiart (1901), and other works upon Opisthobranch embryology, together with those of importance pertaining to the remaining molluscan groups, Annelids and Platodes, will be considered during the course of this paper.

A good general account of spawning habits of Nudibranchs is found in Alder and Hancock's "Monograph of the British Nudibranchiate Mollusca" (1845).

Maturation and Fertilization.

It is not the purpose of this paper to discuss in detail the maturation processes of the egg, but a few words in that connection may not be amiss. Maturation appears to have begun at the time of laying, since the first polar spindle is already formed in all eggs examined. In fig. 1 the chromosomes have moved to opposite ends of the first maturation spindle, and at a slightly later period, fig. 2, the sperm may be seen making its way through the yolk globules toward the upper pole. In a large number of sections examined the sperm is seen to have entered at some point below the equator of the egg, though apparently never directly at the center of the vegetative pole. The chromatin of the sperm nucleus is but slightly evident at this time, but astral radiations are strongly marked in the surrounding cytoplasm. The clear more protoplasmic substance of the egg becomes aggregated principally around the first polar spindle and in the neighborhood of the sperm nucleus, though long strands of finely granular protoplasm extend through nearly the entire egg, forming the astral rays. The yolk, which is in the form of rather small yolk globules, encroaches closely upon these centers, but is not, as a rule, found within them. As the first polar body arises, the upper surface of the egg becomes distinctly indented immediately above the first polar spindle and from this depression the first polar body emerges, bearing with it the distal end of the first maturation spindle, which rises as a whole toward the upper surface of the egg. During this process the sperm nucleus and aster remain in relatively the same position as before. There appears to be no telophase to this division, but without entering into a rest stage the second polar body is given off. This arises from the same place as the first, pushing the latter farther outward or somewhat toward the side (Pl. XXI, fig. 3). Both finally lie in the slight depression at the surface of the egg. The female nuclear elements still left within the egg then come to rest, at first lying closely against the cell wall below the polar bodies. The first polar body does not divide again immediately and may never do so, though usually at a later period three are found. If it remains undivided the first polar body exceeds the second in size.

With the close of maturation the sperm nucleus is seen to have moved upward through the yolk; its chromatic elements have become more evident several large nucleoli being present. The same is true of the female pronucleus. They now approach each other, and come to lie with their nuclear walls closely appressed (fig. 4), the egg nucleus lying

above and the sperm, which is the smaller, below. The clear granular protoplasm of the egg together with the sphere material surrounds both nuclei. The upper surface of the egg has resumed its former rounded outline, pushing the polar bodies farther outward. Their connection with the egg does not appear to be a very intimate one for they do not, in most cases, maintain at a later period any fixed relation to the poles of the egg and so are of little value in orientation, though they are often found in the apical region.

Unsegmented Egg.

The unsegmented egg of *Fiona* averages in diameter 80 micra with polar axis slightly less. The two polar bodies lie at the animal pole. Though the ovum is rather densely yolk-ladened, the yolk globules are of such small size that in future cleavages they tend to become more equally distributed among the resulting blastomeres than is the case with eggs containing yolk in larger spheres. The yolk which encroaches upon the more protoplasmic environs of the nucleus consists of smaller globules, but otherwise its distribution throughout seems quite equal.

The universal distribution of yolk to all the cells of the segmenting egg of *Fiona* is probably to be correlated with the smaller size of the individual yolk globules. It is safe to infer that each yolk body in an egg, whether it be small or large, is surrounded by a thin layer of protoplasm. In eggs containing a relatively larger number of yolk globules or, in other words, where they are small in size, a greater amount of cytoplasm will be distributed throughout the egg, when compared with that aggregated around the nucleus, than is the case when the single aggregations of yolk are large. When this is the case and division occurs the whole mass will be more influenced by nuclear and cytoplasmic divisional activity than when the cytoplasmic constituents are more definitely separated from the yolk. Just what this activity is we do not know, but a comparative study of eggs showing large macromeres with those like *Fiona*, in which cleavage is more equal, will, I think, show that in the former case the individual yolk masses are much larger than in the latter, thus allowing for greater cytoplasmic influence where more finely divided yolk is found. The more equal division of cells naturally results in a wider spread of yolk through the developing organism, and it might also be added, as a corollary to this, that the absorption of more finely divided yolk is doubtless much more readily accomplished than where large globules are found, thus rendering it possible that such a wide distribution should occur in cells not alimentary in function.

Before segmentation the nucleus lies but slightly above the center of the egg, having moved downward with its surrounding mass of granular protoplasm. An extremely thin and easily ruptured vitelline membrane surrounds the egg, and on account of the delicacy of this membrane no micropyle is present. Usually one but often two or three eggs lie together within a roomy egg capsule, containing also a fluid substance which does not coagulate in reagents. In unstained fixed material, and also doubtless in the living state, the eggs are quite opaque from the yolk which they contain.

First Cleavage.

The first cleavage is initiated by nuclear rupture and increased evidence of stellar radiation. With the formation and elongation of the spindle the surrounding yolk spherules give place to the more protoplasmic constituents of the cell which form the immediate nuclear environs. The spindle as it elongates moves somewhat farther downward in the egg and lies but slightly above the equatorial plane. In length it measures about half the diameter of the egg. From the first constriction is almost equally marked all around the egg, though slightly greater at the animal pole. After the chromosomes have separated and are moving toward the opposite ends of the spindle, one end appears somewhat higher than the other (fig. 5), a position which would indicate a spiral trend of cleavage; but this is not evident in the telophase and completed division, for in the two-cell stage the nuclei lie directly opposite each other.

As in the usual history of cleaving eggs, the resulting blastomeres are at first much rounded, but as their nuclei form they become closely pressed together, forming a flattened contact surface between which no cleavage cavity exists (fig. 6). The nuclei, together with their surrounding cytoplasm, again approach the upper surface of the egg and lie at rest just beneath the surface on opposite sides of the polar bodies. There is no evidence in their position to indicate a "virtual" rotation before the next cleavage, as is the case in *Crepidula* (Conklin, 1897). The daughter nuclei of the first cleavage becomes much dilated, containing several nucleoli suspended in the chromatin network and surrounded by clear nuclear fluid.

The two blastomeres thus formed are equal or so nearly equal in size that they present to the observer no mark of distinction, and it can only be conjectured which will form the anterior and which the posterior region of the larva. Indeed, not until the appearance of the mesentodermal cell at the close of the twenty-four-cell stage can

this distinction be drawn, for until that time all quadrants appear identical, though doubtless cytoplasmic and nuclear differentiation is present. As a result of this similarity of all the quadrants the figures, until the appearance of the mesentoderm cell, have of necessity been labelled arbitrarily. Of course, even in the two-cell stage lateral may be distinguished from terminal areas, for by following succeeding cleavages and marking the relation which the lower polar furrow bears to the first cleavage plane and the later relation of both to the median plane of the embryo, it can be determined that the first cleavage plane is obliquely transverse to the median plane. But not until a later period does posterior become distinguishable from anterior end.

In the formation by first cleavage of two cells of equal size, *Fiona* agrees with a large number of Mollusks and Annelids, among the former of which may be mentioned *Ischnochiton* (Heath, 1899), *Neritina* (Blochmann, 1881), *Crepidula* (Conklin, 1897), *Ercolania* (Trinchese, 1880), *Tethys* (Viguier, 1898), *Planorbis* (Rabl, 1879, and Holmes, 1900), *Limax* (Kofoid, 1895, and Meissenheimer, 1896), and among the latter *Lepidonotus* (Mead, 1897) and *Podarke* (Treadwell, 1901).

Unequal cleavage appears to occur as commonly as equal among Opisthobranchs, examples of which are *Acera* (Langerhans, 1873), *Aplysia* (Blochmann, 1883; Carazzi, 1900), *Umbrella* (Heymons, 1893) and *Philine* (Guiart, 1901).

Second Cleavage.

The second cleavage results in four cells of approximately equal size. The spindles which precede it lie at right angles to the first cleavage spindle. and nearly parallel to each other, the left end of each, however, being slightly higher than the right, showing the læotrophic character of the division. As cleavage proceeds this tendency becomes more marked, the upper or left-hand cells (A and C) lying higher than the right (B and D). In consequence of this the second cleavage planes do not meet in a line at the vegetative pole, but a portion of the original first cleavage plane unites them in the ventral polar furrow ("Querfurche" or "Brechungslinie"), the cells B and D being in contact below, while A and C never meet at the lower pole. At the upper pole no furrow is present in *Fiona*, the four cells all joining in a common central point. As is the rule among Annelids and Mollusks in which the second cleavage is læotropic, the ventral polar furrow taken in connection with the first cleavage plane, bends to the right when viewed from the animal pole, and, *vice versa*, it turns to the left if considered as a part of the second cleavage plane. *Fiona* is no exception to the above

rule, and by observing the position of this furrow the first and second cleavage planes may be kept distinctly in mind until outwardly visible differential changes in the quadrants present other landmarks for orientation.

Origin of Germ Layers.

Segregation of the Ectoblast.

By the next three divisions in which the four macromeres participate the entire ectoblast arises.

First Quartet.—The spindles which precede the appearance of the first quartet of micromeres lie at first nearly radial, their proximal ends being distinctly higher than the distal. As a rule, all four spindles do not show the same stage of karyokinetic activity, though irregularities of this nature are not as yet greatly marked (fig. 9). As division proceeds they turn in a dexiotropic direction and with associated cytoplasmic constrictions four small cells are given off toward the animal pole (Pl. XXII, figs. 10, 11). These, the first quartet of micromeres, are in size about one-fourth that of their parent macromeres. As they round out in shape they are pushed farther toward the right, and finally come to lie in the furrows to the right of the large cells from which they arose. With the completion of cleavage the whole egg again takes on a decidedly rounded contour, the micromeres changing materially in shape, becoming more flattened on their outer surfaces and sharp-angled below to fit the indentations between the macromeres (fig. 14).

Second Quartet.—The second quartet arises læotropically, thus regularly alternating in direction of cleavage with the first. The derived micromeres are but slightly smaller than the underlying cells from which they arise and are pushed strongly toward the left as they are given off. By this movement the four cells of the first quartet are also carried somewhat to the left, though the rotation is not great. All the second quartet cells are alike in size, there being no sign of increase in D quadrant, as is the case with many Annelids and some Mollusks; nor is there marked difference in their time of origin, though in future cleavages of the egg irregularities in the time at which divisions occur in similar cells of the four quadrants become more and more marked. In cytoplasmic structure these cells appear to differ little from their parent macromeres, though probably they contain less yolk. Their ultimate position is opposite and beneath the divi-

sion walls of the first quartet, but they do not appear to become so flattened as their predecessors (figs. 13, 14).

The Trochoblasts.—Before the macromeres again divide the first quartet is seen to be in process of cleavage. There result eight cells of nearly equal size, the more peripheral being slightly smaller than those at the apical pole. The spindles which precede division are læotropically directed, and the lower cells are pushed downward and outward between the second quartet cells and just above the macromeres (figs. 15, 16). These "primary trochoblasts" or "turret cells" do not again divide until about sixty cells are present (Pl. XXV, figs. 33, 38), when they have become considerably flattened and lie between the arms of the forming ectoblastic cross. The fate of these very characteristic cells will be discussed later.

Third Quartet and First Division of Second Quartet.—The first division of the second quartet and the third division of the macromeres occur simultaneously. Each second quartet cell forms two of equal size by a distinctly dexiotropic cleavage, the spindles being from the first inclined in that direction. As may be seen in figs. 17 and 18, these cells do not all divide at exactly the same time, and this lack of regularity is also characteristic of the macromeres. By this division of the second quartet the eight cells of the first are pushed backward dexiotropically so that, in relation to the macromeres, they occupy the same place as when given off. The division of the macromeres results in the four cells of the third quartet. They arise in a dexiotropic manner and are equal in size to the four cells left at the lower pole. From this stage on these latter are "macromeres" in name only, being equalled in size by the third quartet and but slightly larger than the eight derivatives of the second. Nor, indeed, do the macromeres appear at this stage to contain much more yolk than the micromeres. At a later period they are easily discernible from the micromeres by their clear yellow appearance, but as the latter divide much more rapidly and by growth distribute the yolk which they contain over a larger area, while much of it is doubtless absorbed, the preponderance of this material in the individual cells of the endoderm and the larger cells of the mesoderm as well is easily explained. As has been mentioned before, in the larva the amount of yolk in ectodermal structures is quite considerable, showing its wide and universal distribution throughout the entire organism.

The twenty-four-cell stage has thus been reached and as yet the egg

is radially symmetrical (Pl. XXIII, fig. 19). At the center of the upper pole lie four "apical" cells, while the "trochoblasts" or "turret cells" extend from them into the angles between the second and third quartet cells. The third quartet and first generation of second quartet lie between them and the macromeres beneath, but from the nature of the cleavages do not form so marked a ring as in *Crepidula* or other Mollusks with large macromeres. The ectoblast has been entirely separated from the underlying macromeres, which contain all of the entoblast and the greater portion of the mesoblast. A small portion of the latter is to be derived, as will be shown later, from the third quartet of ectoblast cells. The egg has become somewhat flattened along its polar axis and within is a small cleavage cavity, which arose during the last few divisions and which later becomes of considerable size. Upon the lower surface the polar furrow remains distinct and offers a convenient means of orientation.

The fact that in Mollusks, Annelids and Platodes the entire ectoblast is separated from the entoblast by the first three successive divisions in which the macromeres participate is a point of similarity of the highest importance in considering the question of the possible genetic relationships of the groups. With scarcely an exception (*Dreissensia*, Meissenheimer, 1901) this is accomplished by regularly alternating spiral cleavages. In most cases the first three quartets of micromeres are small protoplasmic cells and differ widely from the yolk-ladened macromeres, and this is particularly true of the first series being correlated with the later history of the cells which compose it, since in all cases they form the apical pole and the sense organs of the larva. Where much yolk is not present, or the spherules are small, more equal cleavage results, so that the macromeres are reduced in size; as examples may be cited many Pulmonates (*Planorbis, Physa, Limnæa, Limax*) and Lamellibranchs (*Unio, Cyclas, Dreissensia*), *Chiton* and *Ischnochiton* among the Amphineura, *Trochus* for the Prosobranchs and the Opisthobranchs *Tethys* and *Fiona*. The same is true of many Annelids (*Podarke, Amphitrite, Clymenella, Arenicola*, etc.).

Both in size of cells and rate and direction of division the egg of *Tethys* (Viguier, 1898) exactly parallels that of *Fiona* up through the twenty-four-cell stage. The same may be said of *Aplysia* (Carazzi, 1900, and Georgeovitch as corrected by Carazzi, 1900), except for the larger size of the macromeres, particularly the anterior ones, and Carazzi's statement that the trochoblasts arise from division of the first quartet—"con fusi distintamente dessiotropici." Such is, however, not the case, as his figures show. Carazzi has evidently, in some

unaccountable way, become confused with regard to the direction of cleavage of these cells, for in another place, after quoting Conklin's statement regarding the trochoblasts of *Crepidula*, that these cells "continue to rotate in a clockwise direction," he adds "E la sua fig. 16 mostra i fusi dessiotropic". As any one acquainted with cell-lineage work can see by reference to the figure mentioned, the upper ends of the spindles all lie to the left of the lower, and if there be any question as to the ultimate læotropic direction of these cleavages a glance at Conklin's fig. 17 removes all doubt. In *Trochus* (Robert, 1903), *Crepidula* (Conklin, 1897) and *Fiona* the trochoblasts are given off by division of the four cells of the first quartet before the second quartet cells divide. In the case of *Trochus* the second quartet is just being formed when the trochoblasts divide. Moreover, *Trochus* shows no rest stage at twenty-four cells as do the other two, for while the third quartet is forming and the second is dividing for the first time all eight cells of the first quartet again divide, and these cleavages are followed by renewed division of second quartet cells. The mesoblast cell, 4d, does not form in *Trochus* at this time but much later (sixty-four-cell stage), while in *Crepidula* and *Fiona* it appears immediately after a short rest period following the twenty-four-cell stage. The sequence of cleavages of *Planorbis* (Holmes, 1900) up to the twenty-four-cell stage closely follows *Crepidula* and *Fiona*.

Segregation of Ento-Mesoblast.

After a period of rest during which no cells are dividing and twenty-four are present in the egg, cleavage occurs in one of the macromeres. This macromere corresponds to that which has heretofore been arbitrarily designated 3D, and from this period onward the four quartets may be definitely distinguished. The division is læotropic and the larger daughter cell, 4d, will later gradually sink into the segmentation cavity, forming a depression at the posterior end of the vegetative surface in the angle formed by the macromeres 3C and 4D, and otherwise bounded by 3d, 3c and the derivatives of 2d. 4d is thrown toward the left and, therefore, in the direction of the median plane, though at first it does not lie quite in that plane but slightly to the left of it or, in terms of spiral cleavage, to its right (Pl. XXIV, fig. 24). In contradistinction to conditions found in heavily yolk-ladened eggs, this cell takes on from the beginning the position of a middle germ layer coming shortly to lie within the cleavage cavity, though, as will be seen later, its derivatives do not all appear to be mesodermal in character. After all three quartets and also the macromeres with the exception

of 4D have divided, and when there are present about 44 cells (fig. 25), 4d or, as it hereafter will be designated more usually, the mesentoblast, ME, divides dexiotropically into cells of equal size. Before their next cleavage occurs the egg contains about seventy cells (fig. 42). By this division, which is bilateral, one small cell arises anteriorly from each of the large ones (figs. 42, 49). The small cells, E^1 and E^2, correspond to the "Primary Enteroblasts" of Conklin, and will be so designated. Considerable variation may be observed in different eggs as to the later position of these cells, as in some they appear to have moved backward along the sides of the large cells, Me^1, Me^2, from which they arose, but, as a rule, they remain in close relation to 4D, and always in later stages may be seen associated with the derivatives of this cell, from which it is hard to distinguish them (Pl. XXIX, figs. 71, 73). The large cells soon divide again into almost equal parts, though the posterior and dorsal pair (m^1z^1, m^2z^2) are slightly smaller (fig. 71). These latter soon divide again, giving rise to two small cells, z^1 and z^2, which are posterior to the larger (fig. 73). Just before this cleavage the two cells M^1e^1, M^2e^2 divide, giving rise anteriorly and toward 4D to two small cells, e^1 and e^2 (corresponding to the "Secondary Enteroblasts" of Conklin), which lie close to the first pair of small cells, E^1, E^2, the four forming a group of little cells with deeply staining nuclei in close contact with 4D, 5C and 5B. Behind them lie the large cells M^1, M^2. In the nomenclature used these would correspond to "Mesoblastic Teloblasts," but before they begin to function directly as such each again divides, giving off a small cell laterally, and these two cells appear to be dorsally directed toward the cleavage cavity above and to the sides of the enteron, but may remain associated with E^1, E^2, e^1 and e^2. However this may be, the mesoblastic teloblasts soon begin to divide, giving off an irregular row of cells which extend around the gastrula laterally. The cells m^1 and m^2 also behave in a similar manner, their derivatives being closely associated with those of the large teloblasts. In figures 80, 81 and 82 only the derivatives of the latter are shown, the other lying dorsal to them. As the teloblasts and the cells m^1 and m^2 divide they diverge laterally and leave behind and between them the smaller cells E^1, E^2, e^1, e^2, closely associated with the posterior elements of the enteron. When these cells are first given off they lie decidedly above the level of the enteric invagination projecting upward into the cleavage cavity, and while in this position might well be characterized as mesodermal elements; but later they change their position, slipping in between the teloblasts and the posterior cells of the enteron, and by the time the teloblasts begin to separate and wander

toward the sides of the gastrula these small cells, which have been derived from 4d, lie nearer the ventral surface than the cells which form the bottom of the invaginating enteron and closely appressed against the posterior boundary of this region. The small cells z^1, z^2, which are the posterior derivatives of the division of m^1z^1, m^2z^2, also continue to lie near the median line in the posterior region of the gastrula, closely pressed and flattened against the ectoderm.

The later history of the enteroblasts, which I believe are concerned in the formation of the intestine, will be discussed in connection with the development of the enteron.

In comparing the mesoblast formation of *Fiona* with that of other forms, *Crepidula* will be considered first, since in this Prosobranch 4d was first found to contain both entoblastic and mesoblastic material (Conklin, 1897). Here 4d arises when twenty-four cells are present and by a læotropic division. This cell soon cleaves dexiotropically into two of equal size. At the next cleavage there result in *Crepidula* four cells of similar size, the posterior and lower pair being the first enteroblasts, while in *Fiona* it is the anterior smaller cells which are entoblastic. At the next cleavage in *Crepidula* the large cells Me^1, Me^2, which still contain both mesoblast and entoblast, give off smaller purely mesoblastic cells anteriorly (m^1, m^2), while in *Fiona* the larger posterior cells give rise posteriorly to similar cells, though they may not be purely mesoblastic. The next cleavage of M^1e^1, M^2e^2 in *Crepidula* completely segregates mesoblast and entoblast, the cells of the latter lying posterior to the mesodermal elements. This division separates two more small enteroblasts in *Fiona*, which here lie with the first enteroblasts anterior to the large cells, M^1, M^2; each gives rise to another small cell anteriorly in *Fiona* which may be enteroblastic, otherwise from this period on they function as teloblasts of the mesoderm.

From the above comparison it is evident that if we consider the position of the mesodermal and endodermal constituents of 4d in connection with the segmented egg as a whole, directly opposite conditions are found. In *Crepidula* the derivatives of this cell form mesoderm anteriorly and laterally, entoderm posteriorly, while in *Fiona* the reverse is the case. But in both forms, if we consider the position of the enteroblasts not in relation to the egg as a whole, but only in connection with the macromeres with which they are to be associated, it will be seen that in both *Crepidula* and *Fiona* these cells are directed toward the posterior region of the cells 4D, 4C, or their derivatives, and that the reverse relations of the enteroblasts and meso-

blasts in *Crepidula* and *Fiona* is the direct result of epibolic gastrulation in the one case, embolic in the other, which is in turn caused by the quantity and nature of the yolk which the macromeres contain. An intermediate condition is found in *Nereis* (Wilson, 1898). Text-figure 1 (a) shows a sagittal section through the cleaving egg of *Crepidula* after one enteroblast has been separated from the mesoblast. The ectoblast has here but half covered the yolk, and the entoblastic element is thrown downward and backward in the direction in which it must go if it follows the ectoderm over the yolk, and finally reaches a position posterior to the blastopore as that structure is closing (Conklin's fig. 61). In *Nereis*, text-figure 1 (b), the ectoderm has advanced much farther over the yolk when the enteroblasts arise, and here we see that these elements are also directed downward but at the same time anteriorly. The next and last step in their change of position is illustrated by *Fiona*, text-figure 1 (c), in which, on account of its invaginate gastrula, the enteroblasts are not only anteriorly directed, but also at first lie higher than the cells from which they arose.

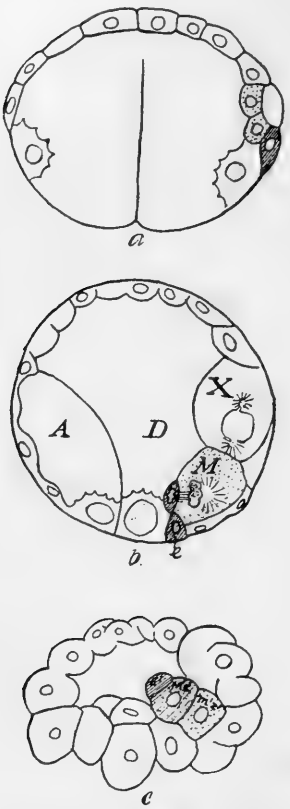

Fig. 1. — Sagittal sections through the gastrulæ of (*a*) *Crepidula* (Conklin), (*b*) *Nereis* (Wilson) and (*c*) *Fiona*. The enteroblasts are lined, the mesoblastic cells stippled.

In *Trochus* (Robert, 1903) the mesoblast arises at about the sixty-four-cell stage by a læotropic division which separates the very large cell 4d from 4D. This cell divides dexiotropically and equally when eighty-nine cells are present. When there are one hundred and eighteen cells, each of the two derivatives of 4d divides, and of the resulting four cells the anterior pair are the smaller. Later the two larger posterior cells divide. Robert has not found endodermal elements to arise from 4d, but does not reject the possibility of such a condition.

As might be expected from their close relationship, a nearer correspondence in the cleavage series is found when we compare *Fiona* with

Umbrella, although Heymons' conclusion regarding the fate of the descendants of 4d is at wide variance with the conditions which are found in *Fiona*. After the cleavage of 4d into equal parts, Heymons states that two small cells are given off from these, so that they lie in the posterior region of the macromeres. It is very evident from his figures that these cells, which would correspond to E^1, E^2 of *Fiona*, at first lie quite dorsal to the enteron and in the cleavage cavity. The large cells next divide nearly equally, the most posterior being slightly smaller and corresponding in size and origin to m^1z^1, m^2z^2. These latter shortly change their position in *Umbrella* exactly as in *Fiona*, for, says Heymons, "Bald beginnt eine interessante Lagerungsverschiebung einzutreten. Es rucken namlich die hinteren Zellen weiter nach dem animalen Pol hin und legen sie vollkommen auf die vorderen auf". While this rearrangement is occurring and after its completion two and later other small cells are given off by the large underlying cells toward the smaller cells originally budded forth. Exactly the same process occurs in *Fiona*—compare Heymons' figs. 23 and 24 with my fig. 71. Heymons' smaller cells M′, M′ (corresponding to m^1z^1, m^2z^2 of *Fiona*), which have moved toward the animal pole of *Umbrella*, do not appear from the account to divide again so quickly as in *Fiona*, but that they later divide teloblastically is evident. As has been mentioned before, the small anterior cells of *Umbrella*, which correspond to E^1, E^2, e^1, e^2, of *Fiona*, at first lie entirely within the segmentation cavity. Figures of later stages, however (Heymons' fig. 29), show that they then lie at a level with the posterior cells of the enteron (D, A′, C′, etc.), and are directly between these and the anal cells. The same relative position is taken by the corresponding cells of *Fiona*.

In interpreting the results of Heymons the above point of view is somewhat different from the comparison of Conklin between *Umbrella* and *Crepidula*, in which he suggests a resemblance and possible similarity of origin between the enteroblasts of *Crepidula* and the teloblastic cells M, M, M′, M′, of *Umbrella*. In both these "are large cells containing a considerable quantity of yolk, about equal in size and grouped in a characteristic way"; but the same may be said of the similar cells of *Fiona*, yet they have no part whatever in the formation of the enteron, though from their appearance I was led to think such might be the case before a knowledge of their later history proved otherwise. The explanation of the whole matter lies in the axial change which the derivatives of 4d have undergone in the forms considered. The posterior macromeres (particularly D) of *Umbrella* are

relatively small, the same result being here obtained as in *Fiona*, in which the entoblastic elements are produced from the anterior rather than from the posterior side of the teloblasts. If any of the descendants of 4d of *Umbrella* described by Heymons are entoblastic in nature they are those which arise in this way, and these are the cells which must be compared with the enteroblasts of *Crepidula* and the small anterior cells in *Fiona*.

Viguier (1898) describes and figures the formation of the mesoderm in *Tethys fimbriata* as similar to that of *Umbrella*, and a comparison of figures will show almost exact correspondence. Like Heymons, Viguier does not consider the derivatives of 4d to be other than mesodermal in fate.

Carazzi (1900) derives both mesoderm and endoderm from the cell 4d ("EM") of *Aplysia*. He states that the cleavage which forms this cell is dexiotropic in direction, and such appears to be the case from his figures. The cell 3A of *Aplysia* is larger than the others, thus throwing 3D so much to the right of the median line that a dexiotropic cleavage is necessary to place the mesentomere upon this line. The divisions of 4d which follow are identical with those of *Fiona*, but Carazzi's conclusions regarding the fate of the remaining blastomeres are quite different. Four pairs of small cells are derived from the two large cells and lie anterior to them. These correspond in position to the four (or more?) enteroblasts of *Fiona*, but by Carazzi are described as mesodermal. Two larger cells have been given off posteriorly and correspond to m^1z^1, m^2z^2 of *Fiona*. From each of these a small cell buds forth posteriorly, the two lying near the ectoderm. These small cells are, according to Carazzi, enteroblasts, and go into the intestine. Cells similar to these in origin and, for the time at least, in position are found in *Fiona* (z^1, z^2) lying closely pressed against the ectoderm in the posterior region of the gastrula. They are small in size, and at a later time I have found it impossible to distinguish them from many small mesodermal cells which crowd that region of the gastrula. If they do not shift their position, they would naturally become involved in the formation of the distal end of the intestine either directly, as lining cells of that organ, or as muscle cells for its walls. One cannot help feeling in comparing the development of the two forms and noting the great similarity in the history of the early derivatives of 4d that their fate is also the same; and the same might also be said of the small anterior elements which Carazzi indicates as mesodermal.

Lillie (1895) concluded that in *Unio* the derivatives of 4d were entirely mesoblastic. The two teloblasts give origin to two small cells

anteriorly which lie near the enteron and are probably concerned in the formation of splanchnic musculature. Similar conditions are found to exist in *Dreissensia*, according to Meissenheimer (1901).

Among the Pulmonates the work of Rabl (1879) is confirmed by Holmes (1900), who finds that all the derivatives of the primary mesoblast are mesoblastic in fate. More particularly he states that the two bilaterally placed teloblasts give rise to a pair of small cells anteriorly, after which the large cells divide into equal moieties. Wierzejski (1897) says of *Physa fortinalis*, "Dass der Modus der Bildung eines Theiles des Mesoderm bei *Physa*, desjenigen aus der Urmesoderm-Zellen fast ganz derselbe ist wie ihn Heymons für *Umbrella* eingehenden dargestellt". In the last stage described the mesoderm consists of twelve cells, a group of six small cells anteriorly placed, behind which are a pair of "Urmesoderm-Zellen" from which they arose, while behind and above lie two other rather large mesoderm cells which have given off a pair of small cells posteriorly. Both in sequence of origin, in relative position and in size this group corresponds to the similar series in *Aplysia* and *Fiona;* but Wierzejski ascribes a mesodermal fate to the whole.

In *Limax* Meissenheimer (1896) describes the cleavage of 4d to a stage in which there are four cells, the anterior pair of which are the smaller. In fate they serve as anlagen for mesodermal structures. Similar conclusions were also reached by Kofoid (1895) on *Limax*.

Heath (1899) has accurately traced the origin of the mesoblast in *Ischnochiton* at the seventy-two-cell stage, and its later cleavage into cells of equal size which lie bilaterally. At a more advanced stage two more divisions were noted giving origin to small cells dorsally and anteriorly. Heath was unable to determine whether these cells were purely mesodermal or partly endodermal.

Mead (1897) describes for the Annelid *Arenicola* two small cells budded off from the bilaterally situated pair of mesodermal cells, and by further division of the large teloblasts these cells are seen later lying at the ends of the mesodermal bands and appear to be mesodermal in fate. The same conclusions were reached regarding *Clymenella*, though in this case the lineage has not been traced so far. In this Annelid the divisions of M^1, M^2 result in cells of nearly equal size, a condition which may indicate a variation in later stages.

In 1897 Wilson, having reinvestigated the history of the second somatoblast of *Nereis*, discovered that the two small cells budded from the teloblasts toward the enteron, to which in his earlier paper (1892)

a mesoblastic fate was assigned, are entoblastic in nature, and the same he thinks probably to be true of *Aricia* and *Spio*.

Child (1900) has found for *Arenicola* that 4d after its first cleavage forms mesoblastic teloblasts, from which later arise two bilaterally placed mesoblastic bands; all these cells are mesoblastic in fate, and it is evident from his figures and discussion that he does not find here any entoblastic material. Though in *Sternapsis* the lineage was not followed so far as that of *Arenicola*, Child reaches the same conclusion, and particularly in the latter case he states that the mesoblastic cell is "purely protoplasmic and without yolk".

In the Annelid *Podarke* (Treadwell, 1901) 4d arises, together with the other members of the fourth quartet, at the sixty-four-cell stage and is equal in size and appearance to them. It sinks inward with the invagination which forms the enteron, divides and lies in close connection with the endodermal cells. By this division from the larger cells four small cells are given to the enteron, while the remaining two are purely mesodermal.

Torrey (1902), in a preliminary on the cytogeny of *Thalassema*, assigns to the two small cells arising from the teloblasts the fate of enteroblasts, in a similar manner as in the Annelids above considered.

Segmentation of the Entoblast.

Shortly after the origin of the mesentoblast 4d, when the egg contains forty-one blastomeres, all the "macromeres" except 4D are seen to be dividing læotropically (fig. 24), with the result that three large cells, 4a, 4b, 4c, are given off from their respective macromeres. These cells are slightly greater in size than those centrally grouped, but are not so large as the cell 4d, and on this account we find that of the four cells, 4A, 4B, 4C and 4D, the last is the smallest, nor does it again divide until over one hundred and fifty blastomeres are present. The position of the fourth quartet may be seen in fig. 25 and those following. When the egg contains over eighty blastomeres, 4A, 4B and 4C again divide into equal moieties, the outer three of which (5a, 5b, 5c) lie to the right of the central group. All these cells have become much flattened and form a comparatively thin roof over the segmentation cavity, into which as yet invagination has not begun. The mesentoderm has sunken completely beneath the external layer and extends forward as far as the center of the cavity (figs. 45, 57). At a much later period, when there are nearly one hundred and fifty cells present, 4a, 4b and 4c again divide (figs. 71, 72, 73), giving off small cells to the left and outwardly ($4a^1$, $4b^1$, $4c^1$). The invagination

to form the enteron has already begun by the depression of the smaller cells which lie in the center of the vegetative pole, while the small cells, E^1, E^2, e^1, e^2, at the anterior end of the teloblasts have become drawn into the posterior region of the invagination (except for some variation, an instance of which is shown in fig. 72), where at this time they help to close that portion of the gastral pit. As the primary enteric cells sink into the cleavage cavity the small cells, E^1, E^2, e^1, e^2, come into close connection with the posterior edges of 5C, 5D, 4a. Thus a more or less complete cup-like invagination is brought about among the entomeres, in which the smaller elements lie at the bottom with the larger ($4a^2$, $4b^2$, $4c^2$) between, and the small cells which have arisen from these latter lying peripheral to them. Above, toward the ventral surface, lie small cells of the second and third quartets around the blastopore opening.

In the formation of the enteric cells the manner in which the fourth quartet arises appears to be characteristic of a number of Opisthobranchs. This quartet is in *Umbrella* (Heymons, 1893), *Aplysia* (Blochmann, 1883; Carazzi, 1900) and *Tethys* (Viguier, 1898), as well as in *Fiona*, larger than the macromeres remaining at the center of the vegetative pole.

The further development of the enteron will be discussed later.

Cleavage History of the Ectomeres.

As has been seen, the ectoblast arises immediately after the four-cell stage by the three successively alternating cleavages in which the macromeres participate, giving rise respectively to the First, Second and Third Quartets of micromeres. The cleavage history of these cells will now be taken up and their ultimate fate, as far as can be determined, considered.

The First Quartet.

The formation of the "turrets," $1a^2$–$1d^2$, and the "apicals," $1a^1$–$1d^1$, leading to the radially symmetrical twenty-four-cell stage, has already been considered. Shortly afterward the apical cells divide in a dexiotropic direction, thus alternating with the preceding cleavage, and by this division the four "basal" cells of the ectoblastic cross arise, while between these and the central point of the egg lie the four small apical cells from which they were derived (fig. 23). Before this cleavage had occurred the upper and dextral cells of the second quartet had in each quadrant given off a small cell in a læotropic direction (fig. 21), which

after the formation of the basals occupy positions just peripheral to them and slightly to the left. These four small second quartet elements are the "tip" cells of the cross, $2a^{11}$–$2d^{11}$, and together with the basals and apicals form the ectoblastic cross.

From the time of its formation and until a late period of cleavage the cross of *Fiona* is a distinctly dexiotropic structure, the apicals of the four arms lying to the right of their respective tips. The cross is thus at the time of its formation (fig. 23) composed of twelve cells, of which the apicals are the central, is radially symmetrical and its anterior and posterior arms lie very near to, if not exactly in, the median plane of the future embryo. In the future history of this structure the tip cells will for convenience be described in connection with the rest of the cross, since they are so closely connected with it.

Before further cleavage occurs in the first quartet the second and third quartets and the macromeres show marked karyokinetic activity, the number of cells in the egg having increased to nearly sixty. The basal cells and the turret cells or trochoblasts then divide simultaneously (fig. 33), though considerable variation in time occurs in different eggs and in different quadrants, it being, however, universally observed that $1d^{12}$ divides last of the basals. It may be noted in this connection that in all species of *Crepidula* examined except *C. adunca* the division in the basal cell of the posterior arm is delayed for a much longer period. The direction of cleavage of the basals $1d^{12}$ and $1b^{12}$ is læotropic and so alternating with the last, those of the other two doubtful; $1a^{12}$ usually shows a læeotropic to radial position of spindle, while in $1c^{12}$ variations are present all the way from læotropic to dexiotropic. After examining a large number of eggs the occurrence of this irregularity was more strongly confirmed, and it thus appears that in this cell, $1c^{12}$, there is a strong tendency, more marked in some cases than in others, toward non-alternation with resulting bilaterality of cleavage in relation to its opposite cell, $1a^{12}$. In *Crepidula*, *Planorbis* and *Neritina* the cleavage of all these basal cells is non-alternating, while in *Umbrella* it is regularly alternating.

In *Fiona* it would appear that we have an intermediate condition in which, though regular alternation is found in the anterior and posterior basal cells, the two lateral, particularly $1c^{12}$, show a tendency toward non-alternation under the influence of approaching bilaterality. It is just at this time that the first distinctly bilateral cleavages occur in two cells of the third quartet in the two posterior quadrants, $3d^1$ and $3c^1$ (figs. 31, 32), and this suggestion of bilateral divisions of the cross may be correlated with them. However, the influence toward bilater-

ality must be very slight, as the radial symmetry of the upper pole is not disturbed to any appreciable degree.

By the divisions of the basal cells above described each arm of the cross is composed of four cells—an outer tip cell ($2a^{11}$–$2d^{11}$), next to it the "middle" cell ($1a^{122}$–$1d^{122}$), an inner "basal" cell ($1a^{121}$–$1d^{121}$), which is larger than its sister middle cell, and an apical ($1a^{11}$–$1d^{11}$).

Synchronously with the cleavage of the basals occurs that of the turrets, the cell of this series in each quadrant dividing into two of nearly equal size, the outer being the smaller. All divisions are dexiotropic and alternating with those by which these cells arose (fig. 33).

Comparing the cleavage of the turrets with conditions found in other forms, it will be noted that considerable variation exists. While in *Fiona* these cells divide when there are about sixty blastomeres in the whole egg, in *Umbrella* (Heymons) approximately seventy are present; like *Fiona* all four turrets divide at relatively the same time. In *Crepidula* the anterior trochoblasts do not divide until there are over one hundred cells in the egg, and Conklin states that he believes the posterior ones never divide. The trochoblasts of *Trochus* (Robert) arise very early, at the sixteen-cell stage, and have all divided when there are thirty-two cells present. In *Planorbis* Holmes finds them in division at about forty cells, and *Limax* (Kofoid) shows a similar condition. In *Unio* (Lillie) there are about fifty cells, while in *Ischnochiton* (Heath) but thirty-two, when the "primary trochoblasts" of the latter form divide. Thus *Fiona* appears to occupy an intermediate position in relation to these and other molluscan forms in which the time of cleavage of these cells has been determined.

Division next occurs in the cross at a stage of about eighty-four cells and results in the division of the apicals into eight small cells, of which those lying centrally form the "apical rosettes" ($1a^{111}$–$1d^{111}$), while the outer series are the "peripheral rosettes" ($1a^{112}$–$1d^{112}$) of Conklin. Direction of cleavage is læotropic, and of the resulting cells the outer are the larger (Pl. XXVII, fig. 53). Shortly after the rosette series are established the basal cells of all arms divide again, the posterior one last. In the anterior quadrant the spindle and resulting cells, $1b^{1211}$ and $1b^{1212}$, lie radially in the lateral arms, the division of $1c^{121}$ is læotropic, that of $1a^{121}$ dexiotropic, again showing bilateral influence, while in $1d^{121}$ the spindle is so strongly turned in læotropic direction that the resulting cells lie transversely across the posterior arm (figs. 56, 62). While this last cleavage of the basals is being accomplished a similar process is seen in the four inner trochoblasts ($1a^{21}$–$1d^{21}$), result-

ing in eight cells of equal size and occurring at relatively the same time in all four quadrants.

With the completion of the above-described divisions the large number of cells of similar size at the upper pole of the egg makes their exact lineage difficult to follow, so that it is desirable to make here some comparisons with the structure and development of the cross and trochoblasts in other forms, and to bring together the results already obtained before proceeding to more uncertain ground. In formation the cross of *Fiona* arises in the same manner as in *Umbrella* and *Planorbis*, by the completion of the tip cells before the basals; and in this it differs from *Neritina* and *Crepidula*, where the tip arises shortly after division has occurred to form the four basal cells. In *Trochus* the tips are relatively late in appearing, as the basals have completed their cleavage before these cells arise. At the first cleavage of the basals another striking similarity to *Umbrella* is found, for in this Opisthobranch the cleavage is læotropic, while in *Crepidula* and *Neritina* it is dexiotropic, thus breaking the law of alternating cleavages; and likewise in *Planorbis* with reversed type the division is læotropic and non-alternating with the preceding. *Trochus* shows an extremely marked læotropic division of these cells, so much so, in fact, that the resulting cells lie almost transversely. In *Fiona* the anterior and posterior basals are distinctly læotropic in origin and so regularly alternating, while considerable variation is found in the lateral arms, a radial type often occurring with $1c^{12}$, sometimes showing a decided dexiotropic direction of spindle. It would appear from this variation in the lateral arms that *Fiona* shows tendencies toward bilaterality in the first quartet at this time, and such a condition would be in harmony with the bilateral cleavages of the third quartet cells, $3c^1$ and $3d^1$, occurring just previously. However, the radial symmetry of the cross as a whole appears not to be disturbed appreciably, so that though these variations may show either a tendency toward bilaterality or toward entire reversal in all quadrants, as is found in *Neritina*, *Crepidula* and *Planorbis*, this influence has not as yet become sufficiently marked to affect the radial symmetry of the upper pole of the egg to any appreciable degree. In discussing the lack of alternation of these cleavages in *Crepidula* as opposed to alternation in *Umbrella*, Conklin suggests "upon this difference the future recognizability of the cross in the last-named cases (*Crepidula* and *Neritina*) depends". In *Umbrella* the læotropic division of the basals is much more marked than in *Fiona*, but even in the latter case Conklin's prediction is in part, at least, fulfilled, as the cross of *Fiona*, after a slightly older stage than thus far described, becomes so irregular that

its component cells are neither among themselves distinguishable nor may they be definitely separated from the surrounding blastomeres. Of course, this is largely due to the multiplication of the trochoblasts and the similarity in size of most of the cells upon the upper surface of the egg, yet the læotropic twist given to the basal elements at their initial cleavage is largely responsible for that irregularity of contour which so early marks the outlines of the cross. The peripheral ends of the arms of the cross of *Fiona* become strongly twisted to the left, and as the structure becomes older the ends tend to bend around in that direction to a marked degree, greatly confusing their component cells with those arising by multiplication of the trochoblasts. Up to the stage shown in fig. 53 the cross has, with the exception of a slight tendency toward variation in the first division of the basals, been radially symmetrical, but at the next cleavage of the basals the cell of this series in the posterior arm divides so that its daughter cells lie transverse to the longitudinal axis of this arm. In the anterior quadrant this division produces cells which lie radially, while in C quadrant the cleavage is læotropic, in A dexiotropic.

The first indication of transverse splitting of the arms is thus seen to occur in the basal cell of the posterior quadrant. In *Crepidula* the reverse is the case, the anterior and lateral arms alone increasing in width, while the posterior later elongates by radial cleavages. In *Fiona* all the arms become longitudinally split at a later period. The inner and outer rosettes have not yet arisen in *Crepidula* when the splitting begins in the cells, 1a–b–c[122], while in *Fiona* they are present and the egg contains many more cells, the basal cells of the anterior and lateral arms having again divided in such a manner that these arms are lengthened before increase in breadth occurs. The same is true of *Planorbis*. The early splitting of the arms of the cross in *Crepidula* is probably in part due, as Holmes suggests, to the fact that, through pressure, they have become much wider and tend to divide in a direction opposite to this elongation. It might also be suggested that the extreme breadth of the cross of *Crepidula* and the early transverse division of its anterior and lateral arms may be correlated with the presence of a large amount of yolk which must be covered by the ectoblast, while in the posterior region the extensive multiplication of the elements of the second quartet obviates the necessary broadening of the arm which reaches in that direction.

The transverse cleavage of the anterior and lateral arms of the cross of *Fiona* occurs shortly after the initiation of a similar process in the posterior arm, but it has been found impossible to trace the lineage

of all the cells accurately though, after lateral extension has occurred, the structure may be demarkated from the trochoblasts and underlying second quartet cells. In fig. 75 its structure and probably cell derivation may be seen. Holmes finds for *Planorbis* that the tip cells divide in a transverse direction first, while in *Crepidula* the middle cells are the first to cleave. The tips appear to divide last in *Fiona*. In the posterior arms after the first transverse division most of the cells divide obliquely across the arms, and in this way the arm becomes longer than the other three. While the cross is increasing in lateral extension the outer turret cells of all quadrants divide, so that the four groups each consist of four cells of equal size (fig. 75) lying in the angles formed by the arms of the cross.

The apical pole of the egg at this period shows a slight depression in the region of the rosette series. It is but transient and disappears with the elongation of the gastrula. A similar depression has been observed in *Neritina, Crepidula* and *Trochus*. Whether the structure is normal in *Fiona* is yet doubtful. Robert insists that such is the case with *Trochus*.

The entire formation of the cross of *Trochus* is peculiar. The basals have arisen and divided before the tips appear, and this division of the basals is so directly læotropic as to be practically transverse. At the next cleavage these two cells form an oblong group of four in each arm. The tips which lie peripherally to these groups next divide, the cleavages of $2a^{11}$ and $2c^{11}$ being bilateral, the first of this nature to occur in the egg.

From the cases cited above of the manner of formation of the ectoblastic cross of Mollusks, it will be seen that this characteristic structure shows great diversity of details throughout the group, though fundamental similarity is evident. Some of the probable causes of such variation are (1) varying amounts of yolk, leading to early lateral extension of the arms in those forms possessing yolk-ladened entomeres, and (2) differences in the manner and rate of development of the trochoblasts, correlated with the later structure and functional importance of the locomotor organ to which they largely give rise. The radial arrangement of blastomeres around the apical pole of the cleaving egg is primarily the result of successively alternating spiral cleavages, and a similar arrangement may be expected in eggs which exhibit this mode of division. A definitely marked cross does not always arise from such an arrangement of blastomeres, as, for example, in Polyclad cleavage, so that this but suffices as a partial explanation. Regarding the form of the crosses of Mollusks and

Annelids Conklin says: "The cross and rosette series are the direct result of the *position, size and shape* of their constituent cells". The *original position* of cells resulting from regularly alternating spiral cleavages is a function of that mode of division. The *shape* of cells depends largely upon the relations which they bear to one another. Their *size* is not so easily explained, and upon this factor depends, to a large extent, the varying forms of crosses met with in different instances. If it be supposed that the original arrangement of the upper pole cells of Mollusk and Annelid eggs was radial in form, the modifications which have arisen in the two groups may, in part at least, be referred directly to the size of the cells comprising that area. The importance and early development of the trochoblasts of Annelids has resulted in encroachment upon that area which in the segmenting eggs of these forms corresponds to the cross region of Mollusks. As a result the "intermediate" series of Annelids, corresponding to the molluscan cross cells, lack the prominence characteristic of the same cells in the latter group. Moreover, it is interesting to note that such a Mollusk as *Ischnochiton*, which in the development of its trochoblasts and prototroch shows a condition intermediate between Mollusks and Annelids, also exhibits a cross which is intermediate in character. Though the trochoblasts have been taken here as an example of the influence which variation in size or rate of division may have upon the primitive arrangement of blastomeres in the spirally cleaving egg, it is doubtless true that other cells may in like manner undergo modifications which will result in similar rearrangements.

Thus it may be concluded that the group of cells constituting the cross owes its radial arrangement primarily to the form of cleavages by which it arose, but that the cross as a definitely marked structure is the result of variations in the size, shape and rate of division of the cells comprising or surrounding it, these variations leading, on the one hand, to the formation of the molluscan cross; on the other, to the annelidan.

Second Quartet.

While the egg is yet radially symmetrical and its blastomeres number twenty-four, the original second quartet cell of each quadrant has divided in a dexiotropic direction into cells of equal size. After the mesentoblast has arisen, but before the basal cells of the cross are formed, all of the second quartet cells divide in a læotropic direction, the upper four giving off the four tip cells ($2a^{11}$–$2d^{11}$) toward the upper pole, while the lower four give origin to small cells resembling the

tips in size, which are directed toward the vegetative pole (Pl. XXIII, figs. 21, 22, 23, Pl. XXIV, fig. 24).

The second quartet at this time consists of four similar groups of cells, each group consisting of two large cells, $2a^{12}$–$2d^{12}$ and $2a^{21}$–$2d^{21}$, lying together, with the smaller cells above and below. The two large cells in all four quadrants, $2a^{12}$–$2d^{12}$, $2a^{21}$–$2d^{21}$, next divide almost simultaneously. The direction of cleavage of the right upper cells ($2a^{12}$–$2d^{12}$) is dexiotropic, and of the resulting cells the upper ($2a^{121}$–$2d^{121}$) are slightly larger than the lower ($2a^{122}$–$2d^{122}$), the divisions being identical in all four quadrants. Synchronously with these divisions cleavage spindles appear in the other large cells of the second quartet ($2a^{21}$–$2d^{21}$). Of the resulting cells the lower are much the smaller. In direction the cleavages are probably all læotropic and therefore non-alternating, though in C and D quadrants the spindles are almost meridional in position, and the cleavages horizontal. Figures 28, 29, 30, 31 and 32 show these divisions in the different quadrants.

The lack of alternation found in the above instance may be explained as the direct result of the relative sizes of the foregoing derivatives of the second quartet and the positions in which they lie. By an examination of fig. 30 it will be seen that should the two large cells, $2c^{12}$ and $2c^{21}$, have divided in the same direction a diagonal row of cells would have been the result, with great pressure against one another and upon the cells in the first and third quartets at the ends of the row. Lack of alternation in direction of cleavage in one of the cells would relieve this pressure, and this is the actual condition found. Such an explanation appears to fit this individual case of non-alternation, but no generalization may be made, as in many other instances the cleavage of blastomeres appears to follow no rules of mutual pressure and can be explained on no grounds so simple.

Division again occurs in this quartet at a stage of about eighty cells and great variation in time is marked in their occurrence.

The following table shows the average sequence observed in the different quadrants, though any one egg may show marked variation from the tabulated result:

	1st.	*2d.*	*3d.*	*4th.*
2a	121	211	122	212
2b	121	211	212	122
2c	121	211	212	122
2d	211	121	212	122 (or 22)

The table should be read: In A quadrant $2a^{121}$ cleaves first, $2a^{211}$ second, $2a^{122}$ third and $2a^{212}$ fourth. In B quadrant, etc. Cleavages in A quadrant are found in figs. 50, 58 and 63; in B, figs. 52 and 59; in C, figs. 44, 48, 54, 60 and 65; in D, figs. 47, 51 and 61.

The divisions of $2a^{121}$–$2d^{121}$ are læotropic in all quadrants, of $2a^{211}$–$2d^{211}$ universally dexiotropic, of $2a^{212}$–$2d^{212}$ everywhere dexiotropic, while variation is found in the direction of cleavage in the cells $2a^{122}$–$2d^{122}$. Of these latter a decidedly læotropic direction is found in B quadrant, horizontal to dexiotropic in D, horizontal to læotropic in A and approximately horizontal in C. With regard to the size of the derivative cells, it may be said in a general way that variation is evident. More particularly considered the following conditions are found to prevail. The divisions of $2a^{121}$, $2c^{121}$, $2d^{121}$ result in cells of equal size, while in the case of $2b^{121}$ the upper cell $2b^{1211}$ is much smaller than $2b^{1212}$; $2a^{211}$, $2b^{211}$, $2d^{211}$ form upper small and lower larger parts, while $2c^{211}$ divides equally; $2b^{212}$, $2c^{212}$, and $2d^{212}$ show similar divisions into upper small and lower large cells, while $2a^{212}$ remains so long undivided that its derivatives are uncertain; $2a^{122}$–$2d^{122}$ divide equally.

As a result of the foregoing cleavages the second quartet contains in all approximately forty cells. The irregularities which have characterized the preceding divisions are increased in number as cleavage continues, though until a much later period all four quadrants show relatively the same number of cells for this quartet. If figs. 67–70, representing the different sides of the same egg, be examined it will be seen that in A quadrant $2a^{1212}$ has divided dexiotropically, while $2a^{2112}$ has divided horizontally; quadrant B shows no further multiplication of elements; in C quadrant, $2c^{1211}$ is in process of division, while $2c^{2111}$ and $2c^{2112}$ have both given off small cells toward the upper pole; D quadrant remains as before.

At a stage in which there are six cells of the second quartet in each quadrant in *Crepidula* these groups very closely resemble the similar ones of *Fiona*. When there are four cells in each group in *Crepidula* the larger middle pair divide and, as in *Fiona*, one of them shows lack of alternation; but in *Crepidula* the direction of the cleavage is slightly læotropic in the right cell and dexiotropic in the left, while just the opposite is true of *Fiona*. *Planorbis* shows a group of second quartet cells in each quadrant, which may be said in this sinistral form to be almost the mirrored image of the same cells of *Fiona*, though the tips and the corresponding cells at the lower pole are somewhat larger in *Planorbis*, which probably accounts for their earlier division in that form. The large second quartet cells of *Trochus*, as in *Fiona*, show lack of alternation in the left cells of the series ($2a^{21}$–$2d^{21}$), while the right ($2a^{12}$–$2d^{12}$) show regular alternation. The early cleavages in the second quartet of *Tethys* (Viguier, 1898) closely parallel those of the same series in *Fiona*. Viguier has mistaken the lower elements of this quartet, $2a^{22}$–$2d^{22}$, for members of the fourth, as Robert has pointed out. Further note of the errors in this paper will not be taken here, since they have been so thoroughly discussed by Robert. Heymons (1893) for *Umbrella* shows the second quartet series up to a stage of six cells in each quadrant, and here also similar conditions are found. Carazzi (1900) figures the egg of *Aplysia*, where each quadrant contains four second quartet cells, and here also is a marked similarity to the other forms considered. The second quartet of *Fiona* maintains a radial symmetry for a much longer period than *Planorbis*, this being the result of similar cleavages in all four quadrants for a much later period than in that Pulmonate. The same may be said of *Umbrella* and *Crepidula*, and, as Holmes suggests, this phenomenon is probably correlated with the earlier development and larger size of the head vesicle of *Planorbis* than of the corresponding structure of *Crepidula*, *Umbrella* or *Fiona*.

The Third Quartet.

Of the three quartets the third is the first to show evidences of bilateral divisions. When the egg has cleaved into twenty-four blastomeres this quartet has but one cell in each quadrant, and these cells do not divide until after the second cleavage of the second quartet. They then all divide in a læotropic direction, but the resulting cells are not of the same size in the different quadrants. 3a and 3b produce cells of equal size, while 3c and 3d give rise to small cells in the direction of the vegetative pole with very large ones above, thus forming an

additional landmark for distinguishing anterior from posterior quadrants (Pl. XXIV, fig. 25). The larger cells of the posterior quadrants, $3c^1$ and $3d^1$, divide next; the spindle in $3c^1$ being dexiotropic and alternating, that of $3d^1$ lævotropic and non-alternating; and this lack of alternation in one of the large cells of the third quartet, taken in connection with the regular alternation of the similar cell on the opposite side of the posterior region of the egg, establishes the first bilateral cleavage (Pl. XXV, figs. 31, 32, 34). Both upper and lower cells of A and B quadrants are the next third quartet elements to divide, the direction in all cases being dexiotropic or in some instances nearly meridional (figs. 37, 40, 41). The lower cells, $3a^2$ and $3b^2$, always divide before the upper, $3a^1$ and $3b^1$, and in all cases cleavage is equal, a group of four similar cells arising in each of the two anterior quadrants. In the posterior quadrants cleavage occurs next in $3d^{12}$, $3d^{11}$, $3c^{12}$ and $3c^{11}$. It will be remembered that when these cells were formed it was through a lævotropic and non-alternating division of $3d^1$ and a dexiotropic and alternating division of $3c^1$, thus producing a bilateral cleavage of similar cells of opposite sides. Now the cells $3c^{11}$ and $3c^{12}$ again divide dexiotropically, thus showing lack of alternation, while $3d^{11}$ and $3d^{12}$ again exhibit distinct lævotropic cleavage and a second failure to alternate. Thus arise in each posterior quadrant two very small cells, $3c^{112}$, $3c^{122}$ and $3d^{112}$, $3d^{122}$, lying below the large ones, $3c^{111}$, $3c^{121}$, $3d^{111}$ and $3d^{121}$ (Pl. XXVI, figs. 43, 44, 45, 47). After these cleavages about eighty blastomeres are present (figs. 67, etc.). When this number has increased to slightly over a hundred, $3a^{21}$, $3a^{22}$, $3b^{21}$ and $3b^{22}$, each gives off a small cell toward the vegetative pole by cleavages which appear horizontal (Pl. XXVII, figs. 57, 59), and these divisions are followed by equal and probably horizontal cleavages in the posterior quadrants of the large cells, $3c^{111}$, $3d^{111}$ and $3c^{121}$ and $3d^{121}$, the former pair always dividing before the latter (figs. 61, 66), so that each posterior group contains seven cells, of which three are small and lie nearest the blastopore, being bounded externally by four large cells, $3c^{1111}$, ^{1112}, ^{1211}, ^{1212}, and $3d^{1111}$, ^{1112}, ^{1211}, ^{1212} respectively.

The history of the third quartet of *Fiona* thus far given adds another to the number of Mollusks in which it has been found that bilateral cleavages first appear in the posterior quadrant, and more particularly in the cells of the third quartet.

The initial divisions of these cells in *Umbrella* appear from Heymons' description to be nearly radial, but his figures show that in the case of 3c and 3d cleavage is lævotropic. The lower products of these cleavages are all smaller than the upper, in which they parallel only the posterior

quadrant cells of *Fiona*. Moreover, these cells, $3c^1$ and $3d^1$, divide again before the anterior ones as in *Fiona*, and these cleavages are the first bilateral divisions described. It would appear from Heymons' figures that the two cells next the median plain lie higher than the outer, and this is the condition found in *Fiona*. If such be the case, these two forms stand in contradistinction to *Crepidula*, in which the median pair are the lower. The cells $3c^{11}$, $3d^{11}$ are the protoblasts of Heymons' excretory cells, and it will be seen later that $3c^{11}$ serves a similar purpose in *Fiona*. It is interesting to note that Conklin says of $3c^{11}$ and $3d^{11}$ that they are "large and clear" and "have the same characteristics in *Crepidula*", though he does not know their fate. Heymons describes divisions at a later stage in the anterior quadrants, while in the posterior $3c^{11}$ and $3c^{12}$, $3d^{11}$ and $3d^{12}$ give rise by horizontal divisions to small cells which lie next to $3c^2$ and $3d^2$—these latter in exact correspondence with *Fiona*.

Of this quartet Holmes says of *Planorbis;* "The first cleavage forms a transition from the spiral to the bilateral type, and subsequent cleavages show a bilateral character in a more marked degree. At nearly the same time the lower pair of cells in the two anterior quadrants and the upper pair of cells in the posterior quadrants divide in a nearly horizontal direction into equal moieties. Later the upper pair of cells in the anterior quadrants divide in the same direction as the lower pair. The lower pair of cells in the two posterior quadrants remain undivided until a much later stage". These divisions closely follow those of *Fiona*, and the same may be said of subsequent ones.

In *Aplysia* (Carazzi) the two third quartet cells of each anterior quadrant divide into equal moieties, while in the posterior quadrants small cells are given off toward the vegetative pole; the same is true of *Fiona*. At the next divisions of $3c^1$ and $3d^1$ "si dividono con fusi transversali, cioè con divisione bilaterale," while $3a^1$ and $3b^1$ remain at rest. Viguier (1898) for *Tethys* describes the initial division of all the four quartet cells as "suivant des plans sensiblement radiaux", the resulting two cells in each quadrant being equal. Later cleavages of this quartet in *Fiona* will be considered under the discussion of gastrulation and secondary mesoderm formation. Bilaterality appears late in the cleavage of *Trochus*. The first divisions of this nature do not occur until the ninety-seven-cell stage, and are concerned with the cells $2c^{11}$ and $2a^{11}$. This is the first violation of Sachs-Hertwig's law of alternatingly perpendicular cleavages. The cleavages of the third quartet are very tardy in this Prosobranch, for when there are as many

as one hundred and fifty cells present this quartet consists of but four cells in each quadrant.

Gastrulation.

With the beginning of gastrulation, marked differences appear in the cleavages of the quadrants and the radial symmetry of the egg as a whole gives place to a more and more distinct bilaterality. In the posterior region, particularly among the cells of the second quartet, great divisional activity and growth takes place; while the same series in A, C and B quadrants show relatively slight increase when compared with the derivatives of 2d. It has been impossible to follow the lineage, except in particular instances, from the time these cleavages begin, as most of the cells of the gastrula of *Fiona* are so similar in size and appearance and the number becomes so great that individual identification is limited to special cases. However, by continued observation of successively developing stages one becomes familiar with the cell groups which will later give rise to various organs and, aided by a few landmarks, may in most cases follow the organogeny with approximate if not absolute certainty.

An examination of figs. 69 and 70 will show that $2b^{1212}$ and $2b^{2112}$ have divided again, and shortly afterward cleavage occurs in a number of other cells, $2b^{22}$, $2b^{2111}$, etc. The upper cells of the third quartet in the anterior quadrants lie at first well toward the upper surface, but as invagination proceeds these move around toward the lower side, while an increasing number of second quartet elements are found separating the first from the third quartet at the anterior as well as the posterior end of the gastrula. Meanwhile the second quartet cells in the median posterior region (derivatives of 2d) have multiplied very rapidly, and by causing increase in the surface area of the gastrula in this region have pushed the apical pole several degrees forward. Not only have the posterior second quartet cells increased in numbers but also in size, marking out at an early period the region from which the shell gland will develop. The second quartet groups which lie laterally below the ends of the lateral arms of the cross also grow in extent and numbers, this being more particularly true of those which abut upon the enlarging cells of the same series in D quadrant.

The history of the third quartet has thus far been followed to a stage when its members in each anterior quadrant number six, of which four are large and two small cells, while in each posterior quadrant the group comprises seven cells, three of which are small and four large. By approximately horizontal cleavages of the upper cells in the two

anterior quadrants four cells of equal size are formed in each quadrant, and as the blastopore continues to narrow these cells migrate as a group in each of the two anterior quadrants, approaching the blastopore and slipping over the cells $3b^{211}$ and $3b^{221}$, $3a^{211}$ and $3a^{221}$, which lie between them and the smaller cells of the same series (Pl. XXIX, figs. 68, 69). During this period the third quartet blastomeres of the posterior quadrants remain as before.

The blastopore thus becomes entirely surrounded by the second and third quartet elements, of which the third are much more numerous, having the small cells $2a^{22}$–$2d^{22}$ or their derivatives wedged in between them on the median and transverse line. The gastrula, taken as a whole, is much flattened dorso-ventrally and is at first shorter in its longitudinal than transverse axis. The blastopore assumes a slit-like form, its longitudinal axis corresponding to the future longitudinal axis of the embryo.

The next important change to be observed is the origin of the

Ecto-Mesoblast.

As the cells $3a^{111}$, ^{112}, ^{121}, ^{122} and $3b^{111}$, ^{112}, ^{121}, ^{122} continue to move toward the blastopore, the cells which they are covering over $3a^{211}$, $3a^{221}$ and $3b^{211}$, $3b^{221}$, sink downward into the segmentation cavity. As this occurs they all four divide, giving rise externally and in the direction of the blastopore to four small cells, $3a^{2112}$, $3a^{2212}$ and $3b^{2112}$, $3b^{2212}$, while the larger daughter cells continue to retreat beneath the overgrowing ectoderm (fig. 74). These larger cells, $3a^{2111}$, $3a^{2211}$, $3b^{2111}$ and $3b^{2211}$, are the source from which the secondary mesoderm is derived. They later divide, as may be seen in fig. 78, and begin at once to form two bands of several cells each, which lie in the antero-lateral region of the gastrula and later in the anterior head region of the larva.

Since the discovery by Lillie in 1895 of mesoderm which arose from the ectoderm in the Lamellibranch *Unio*, various other cell-lineage workers have arrived at similar conclusions concerning other forms. As is well known, Lillie found that the larval musculature of the Glochidium arose from a cell of the second quartet, 2a, which in cleavage gives rise to a cell toward the segmentation cavity, the descendants of which are mesodermal in fate. Conklin's results, published in 1897, gave evidence that in the Gasteropod *Crepidula* ectodermal mesoderm arose in three quadrants, in this case also from the second quartet (2a, 2b and 2c), but appearing much later then the "larval mesoblast" of Lillie, so late, in fact, that the exact cell origin could not be traced.

In 1897 Wierzejski showed that in the sinistral Pulmonate *Physa* secondary mesoblast arises from certain derivatives of the third quartet (3c and 3b), and similar conclusions were reached in the same year for *Planorbis* by Holmes, 3c and 3b here also giving rise to cells which sink into the segmentation cavity.

The formation of the secondary mesoderm in *Fiona* is strikingly similar to its manner of origin in *Planorbis*, as described by Holmes. The following diagram (text-figure 2), showing the cleavage history of the ectomesomeres of the two forms, indicates how close a comparison is possible.

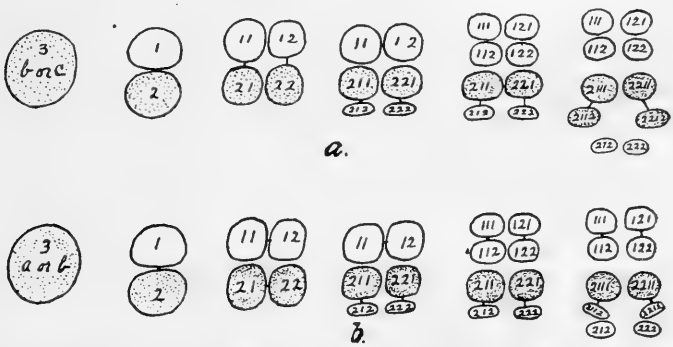

Fig. 2.—Diagrams showing the manner of formation of secondary mesoderm in (*a*) *Planorbis* (Holmes) and (*b*) *Physa* (Wierzejski) and *Fiona*. The cells containing secondary mesoderm are stippled.

It will be noted that four cells of each anterior quadrant are mesodermal in *Planorbis*, while in *Fiona* only two have this fate, the smaller cells, $3a^{2112}$, ^{2212}, and $3b^{2112}$, ^{2212}, of *Fiona* remaining in the ectoderm. For *Physa* Wierzejski came to similar conclusions, but here there is even closer correspondence, for the cells $3b^{2112}$, ^{2212} and $3c^{2112}$, ^{2212} of *Physa* remain in the ectoderm exactly as they do in *Fiona*. According to the nomenclature used by these two investigators secondary mesoblast arises from quadrant B and C, while in the dextrally cleaving egg of *Fiona* it comes from quadrant A and B. Holmes and Wierzejski have attempted to use the same sequence of lettering for sinistral forms as that commonly employed for the dextral, and have thus been led into error, Holmes particularly arguing for a non-homology of cells upon this score. When the dextral or clock-wise sequence is employed for a sinistral form this difference in designation necessarily results if the cell which is to give rise to the entomesoblast be labelled D. The more natural and logical method is to label the cells of a sinistral form in an anti-clock-wise sequence, as Crampton (1894) has

very wisely done for *Physa.* Robert (1903), in his excellent paper on the development of *Trochus,* which has just reached this laboratory, calls attention to the above and confirms opinions which had already been embodied in this paper. Animals which are sinistral, or reversed in their larval and adult stages, develop from eggs which are likewise reversed in their cleavage, and the designation of the blastomeres of the egg should coincide with the condition of the adult, if any homology of cells exists. The eggs of sinistral Gastropods have probably at an early stage in their ovarian development undergone complete cytoplasmic and nuclear inversion, for only by such a process can the reversed condition of the larvæ and adults be understood or the reversal of direction of the cleavage spindles be explained, and if such an inversion be postulated, corresponding reversal of sequence in nomenclature must ensue.

Meissenheimer (1901) describes in *Dreissensia* a cell lying in the cleavage cavity just under the First Somatoblast derivatives, but which, he says, does not come from this group, though he is sure it is of ectodermal origin. It later divides and forms muscle fibers. Similar conditions appear to be present in *Cyclas* (Zeigler, 1885). In the fresh-water Prosobranch *Paludina* teloblastic pole cells are not found. Scattered mesenchyme cells occur, and Tönniges (1896) states that these have been produced from cells which lie in front of the blastopore. If this be the case, the formation of mesoderm in *Paludina* is similar to that of the secondary mesoderm of other Mollusks.

In *Dinophilus* (the cleavage of which is, from work now being done in this laboratory by Dr. J. A. Nelson, typically annelidan in character) Schimkewitsh (1895) appears to have recognized ecto-mesoblast, for he says: "Gleichzeitig (with the proliferation of Urmesodermzellen) aber findet auch eine Immigration der Ectodermzellen in der Vordertheil des Embryos statt, und es wird durch diese Zellen eine Mesemchymanlage gebildet".

In the Annelid *Aricia,* Wilson (1897) discovered mesoderm arising from the two posterior quadrants which could not be derived from the pole cells, and which he located as coming from "either the second or third quartet" (*i.e.,* from c^3 and d^3 or from c^2 and c^3). These conclusions were strengthened by a preliminary account of Treadwell (1897) on the cell lineage of *Podarke,* in which he derives secondary mesoblast from the third quartet (3a, 3c and 3d), and these results are confirmed in a later and more elaborate paper (1901). The account of the mesoderm formation given by Eisig (1898) for *Capitella* differs widely from the results of most workers on annelidan and molluscan embryology.

Here the definitive mesoblast is said to arise from 3c and 3d, which would be in correspondence with Wilson's "ecto-mesoblast," while what Eisig considers "larval" or "secondary" mesoblast comes from that portion of 4d which Wilson and Treadwell found in *Nereis* and *Podarke* to form part of the wall of the enteron. These results have, it seems justly, been called in question, though the careful investigation from which they spring certainly gives credence to their accuracy. Treadwell (1901) has called attention to certain figures (Pl. XXXIX, fig. 42, to Pl. XL, fig. 49) of Hatschek on *Eupomatus*, which show "scattered muscle cells in the upper hemisphere of the larva, which could hardly have come from the feebly developed mesoderm bands at the posterior end of the body", and suggests that they are of secondary origin; and he likewise calls attention to the figures of Drasche (1884) for *Pomatoceros* which show similar conditions, though neither of these investigators appears to have realized their significance. In a preliminary paper on the development of the mesoblast in *Thalassema*, Torrey (1902) derives ecto-mesoblast from all three quartets. "In all there are at least twenty primary cells of this character, but of them only ten, arising from the first and third quartets, develop into functional mesenchyme, while at least ten degenerate and are finally absorbed by the entoblasts." The greater part of the functional ecto-mesoblast comes from three cells of the third quartet (3a, 3c and 3d) which correspond closely to those which produce secondary mesoblast in *Podarke*. All of the cells arising from the second quartet and which sink into the segmentation cavity are rudimentary and in the end entirely degenerate, thus recalling Wilson's similar conclusions regarding the "rudimentary" cells of the definitive mesoblast of *Aricia* and *Spio*. At least six derivatives of the seven ecto-mesoblast cells which Torrey derives from the first quartet have a similar fate.

The mesoderm of Platodes, Annelids and Mollusks has of late years been subject to much study, and various theories have been propounded regarding the significance of the manner of formation of the middle germ layer of these groups. Without entering into a prolonged discussion with regard to this question, a few of the more general points may be mentioned. The results above tabulated and my own observations lead to the conclusion—which is, of course, not here stated as new—that the primitive mesoderm of these groups is represented by that which arises from the ectoderm, and which is alone found in the Polyclad (Wilson). The suggestion of Wilson that upon this hypothesis ecto-mesoblast might well be found arising from all three quartets of ectomeres has just been verified by the work of Torrey, and shows that

in this respect *Thalessema* presents an ancestral condition similar to that of the Polyclad, though this does not necessarily imply close genetic relationship. Moreover a descending series may be formed both among Annelids and Mollusks of forms in which the presence of ecto-mesoblast gradually merges into conditions in which it has totally disappeared, showing that in these groups ectodermal formation of mesoderm is on the decline. The increasing number of cases reported in which ecto-mesoblast is larval in fate tend also to support this conclusion, nor do the results of Meyer, showing that much of this building material is used for adult structures, offer a serious objection, since it is a well-known fact that nature is not prodigal of the living substance on which it works, and the secondary application of ancestrally obsolete material is a fact of almost universal occurrence. Nor can I see that the later origin of ecto-mesoblast necessarily indicates its late phylogenetic appearance, as some have argued, since the early origin of ento-mesoblast, if associated with the future elongation of the animal, might well be supposed to be directly explained by the precocious segregation of this layer in those forms in which its development is so intimately connected with future growth and development. The early appearance and teloblastic growth of ento-mesoblast in the posterior region of Annelids and Mollusks has directly led to decrease of the radially appearing mesoblast. The Polyclad, which shows no endo-mesoblast, has failed to develop such a formation, though a tendency in that direction may be appearing, being marked by the bilateral division of one of the endodermal derivatives (Wilson). The fact that ecto-mesoblast as well as ento-mesoblast has been shown among Annelids to arise from the same quadrant (*Aricia, Podarke, Thalassema*) argues, it seems to me, conclusively for an entirely separate mode of origin of the two.

Closure of the Blastopore.

With the segregation of the secondary mesoblast changes appear in the form of the gastrula. Heretofore its shape has been broadly oval, the antero-posterior axis being the shortest, but at this period two regions of growth become manifest leading to marked change of form. The multiplication and growth of cells of the second quartet in the posterior region increase in activity, ever pushing forward the apical pole area, while at the same time the region just anterior to the apical pole is seen to be rising from the surrounding surface, forming a pointed projection, the summit of which lies at the anterior end of the forward arm of the cross (Pl. XXX, figs. 78, 79).

Synchronously with these changes the blastopore continues to decrease in size, being narrowed by overgrowth of cells in that neighborhood. It will be seen by the examination of fig. 78 that the large cells of the third quartet in the anterior quadrants ($3a^{111}$, ^{112}, ^{121}, ^{122} and $3b^{111}$, ^{112}, ^{121}, ^{122}) are all encroaching farther upon the smaller cells of the same series, which have been crowded beneath them at the edge of the blastopore. Posteriorly, derivatives of the third quartet have completely surrounded the blastopore by the division and migration backward of the small cells $3c^2$ and $3d^2$, while more laterally the remaining small cells of this quartet and their neighboring larger cells are crowding around the depression. The second quartet cells, $2a^{22}$ and $2c^{22}$, or their derivatives, yet lie in the lateral corners; but as closure of the blastopore proceeds they are crowded from this position by encroachment of the third quartet both from before and behind, which finally (fig. 79) join each other on the sides. In the anterior median plane, however, a cleft yet remains between the large third quartet cells, and after the inner of these large cells have divided, as shown in fig. 79, cells of the second quartet, represented by the derivatives of $2b^{22}$, still occupy the space between them and there bound the blastopore. Throughout this process the greatest extension of the third quartet is manifest in the area covered by the posterior third quartet groups, and this is doubtless connected with the disappearance from the ectoderm in the anterior groups of the secondary mesoblast. The blastopore closes from behind forward, to which process the larger number of third quartet cells in the ectoderm of the posterior region conduces.

The posterior surface of the gastrula is now covered by large cells of the third quartet, and in the median region by second quartet elements. On the right posterior surface (left when seen from ventral surface, fig. 79) may be seen one very large cell, Ex. ($3c^{1111}$), which will later become the principal excretory cell of the larva. The region anterior to the blastopore has been formed from the second quartet cells of B quadrant which have been pushed backward by posterior and apical growth, space being left for them through the shifting of the large cells of the third quartet already described. The second quartet cells of B quadrant have shown comparatively little division or growth, and thus appear to occupy a relatively smaller space than previously.

The blastopore of *Crepidula* (Conklin) is surrounded by second and third quartet cells, all quadrants contributing. The same is true for *Ischnochiton* (Heath). In *Trochus* (Robert) third quartet cells are

mainly concerned in the closure of the blastopore, though the derivatives of $2a^{22}$–$2d^{22}$ also bound the narrowing opening. *Planorbis* (Holmes) shows a very similar condition, with the exception that $2d^{22}$ is crowded out. In *Fiona* all second quartet cells but a few at the anterior edge of the blastopore are excluded before the opening closes.

Organogeny.

The Velum.

In its earlier stages the velum of *Fiona* is so ill-defined on the upper surface of the developing larva that its study has proved most difficult, and though more time has been spent upon this region than any other portion of the developing organism the results have not been as satisfactory as could be wished. Living material would have been of great value, and the lack of it has been a source of much regret. After the breaking up of the cross the whole external surface of the gastrula, and particularly the anterior end, is characterized by cells of small and nearly equal size, among which there appear scarcely any cells whose size would give them prominence, or cell rows or distinctly marked groups.

In the last stage described under the discussion of the development of the first quartet the area covered by this series of micromeres represents nearly the whole upper surface of the flattened gastrula (fig. 75). The four arms of the cross are split transversely, while in the angles between them lie the four groups of turret cells, each group consisting of four cells of equal size. In axial relation the anterior and posterior arms correspond to the direction of the median plane, while the lateral are respectively right and left. The whole first quartet area is completely surrounded and separated from the third by derivatives of the second. By an increased growth of D quadrant of this series the apical pole and its surrounding area is moved forward in the direction of the blastopore, while at the same time growth of first and second quartet elements in the neighborhood of the tip of the anterior arm of the cross causes that region to become raised, until somewhat later the pointed anterior end so characteristic of many Opisthobranch larvæ is produced (figs. 78, 79, 96). The visible cause of the evagination of the ectoderm at this point may be found in the directions taken by spindles of the dividing cells which produce it, as in most cases they are radially or diagonally directed toward the point of greatest elevation. At this time the archenteron is roughly triangular in outline, the anterior point of the triangle being marked by

the large cell $4b^2$, which remains for a long time in this position and is closely pressed up into this anterior cone. It may thus be possible that the pointed anterior end of the larva is caused by the shape of the enteron, upon which the outer layer is moulded.

At first the terminal point of elevation corresponds in position to the tip of the anterior arm, and is thus formed by derivatives of $2b^{11}$ and neighboring cells. At a somewhat later period the continued growth of the shell gland area pushes the whole apical region forward, so that eventually (figs. 95, 98, 100) this point is carried farther downward on the anterior surface. At the same time continued growth has increased the extent of the whole apical region, so that the anterior end becomes more rounded than pointed, and finally (figs. 101, 102), when the veliger stage is just being approached, a broad rounded contour characterizes the anterior as well as the posterior end of the larva. It is while these changes are taking place that the first evidence of a distinct velar area appears. Early in this period of forward movement the anterior trochoblasts may be seen to the right and left of the anterior end of the forward arm, being distinguished from the derivatives of the second quartet by their smaller size and compact arrangement. They thus, with the tip cell and two other cells behind them (probably $1b^{1221}$, $1b^{1222}$, derived by transverse splitting of the middle cell), form an irregular row across the anterior edge of the first quartet area (fig. 76). Laterally the posterior ends of this semicircle are joined by cells in the region of the tips of the lateral arms and thus meet the posterior trochoblast groups. These latter have grown larger than their corresponding cells in the anterior quadrants, and so are almost indistinguishable from second quartet elements which lie beneath them. On this account it soon becomes impossible to separate them from these cells, and so at a later period, when the velum in this region becomes marked, I am unable to state how much of it is derived from the trochoblasts, though the little evidence at hand indicates that they form the largest portion of it. With change of axis the anterior end of the velum is carried forward (Pl. XXXVII, figs. 95, 98), and the forward end comes upon a level with the antero-ventral surface. A lateral view (fig. 98) shows an irregular row of nuclei (cell outlines are usually indistinct) running downward and backward from the anterior median point, and becoming lost as it continues posteriorly. This row, which has arisen from the anterior trochoblasts, derivatives of the middle and tip cells of the anterior arm and probably tip cell derivatives of the lateral arms, will be designated V^1. Below this band of cells another irregular row may be distinguished composed entirely of second

quartet cells which have lain nearest the first quartet area, and this row, the first appearance of which is indicated in figs. 97 and 98, will be designated V^2, since it corresponds in general to the same cells in *Crepidula* which are designated by that term. Unfortunately the cells in this region have for some time presented no distinguishing marks, without which exact derivation is precluded by their number, but from their positions these lower cells probably correspond to derivatives of $2b^{121}$, ^{122}, ^{211} in the anterior group, and similar cells in the lateral. At a later period (fig. 101) these rows tend to unite to form an irregular line several cells in breadth, distinguishable only by their nuclei. As the stomodæal invagination progresses the velar rows are drawn forward and downward in that direction, and by the growth of the head vesicle they are also pushed downward laterally. It is probable that elements of the second quartet which lie still lower than those already mentioned become involved in the preoral velar area, either functioning directly as ciliated velar cells or taking part in the development of the underlying region of the expanding velar ridge. At the period represented in fig. 103, two irregular rows of nuclei may be observed in the anterior cephalic region above the stomodæum, and these correspond in origin to the rows V^1 and V^2 above mentioned. The postoral velar area is but faintly demarkated in the preparations studied and crosses the ventral region just behind the stomodæum. The cells comprising it are doubtless, in the median region, derived from the third quartet, to which are added second quartet elements more laterally where the postoral velum joins the preoral.

A portion of the velum does not in *Fiona* curve sharply toward the apical pole, as in the case of *Crepidula*, where an anterior branch is formed, but the whole extends backward around the head vesicle, so that this part corresponds in position to the posterior branch of *Crepidula*. This difference will be evident if a comparison is made between figs. 78 and 82 of *Crepidula* and fig. 108 of *Fiona*. In the latter instance it will be seen that the apical pole lies far forward from the posterior ends of the velar edge, while in *Crepidula* the anterior branch curves inward toward the apex, while the posterior branch continues backward around the whole head vesicle, as does the entire velum of *Fiona*.

In *Crepidula* Conklin (*Supplementary Note*, p. 204) finds that the median anterior portion of the first velar row (V^1) probably arises from the divided tip cells of the anterior arm, while laterally this row is continued by the trochoblasts and cells at the ends of the lateral arms. The second row in its mid-ventral region is probably "derived

from the cell identified provisionally as $2b^{22}$, which lies just beyond the median cells of the first row", and he adds, "I have not been able to determine whether any part of the second velar row arises by subdivision of cells of the first; if not this row may include a few of the third quartet ($3a^{111}$ and $3b^{111}$, fig. 56) at the points opposite the anterior turrets". It also seems probable (*Supplementary Note*, page 204) that the cells $2b^{12211}$, $2b^{12212}$ lie outside the first velar row. Fig. 79 shows two large cells between the first and second velar rows, and they appear to represent the major portion of these cells. Smaller derivatives from them may join $2b^{22}$ in forming the median part of the second velar row (V^2). Conklin thus finds that the preoral velum arises from "a few cells of the first quartet, many of the second and possibly a few of the third". I do not believe that the third quartet becomes involved in the preoral portion of the velum of *Fiona*, though doubtless cells from this series are closely connected with it in the stomodæal region and help in the formation of the postoral velum. It will be remembered that in *Crepidula* secondary mesoblast is derived from the second quartet, while in *Fiona* it is furnished by the anterior groups of the third, and in this process the large cells of this series, which have hitherto lain well up on the sides of the gastrula, migrate over the underlying mesoblastic elements and thus become far removed from the region where the velum first appears. The formation of secondary mesoderm in the most anterior second quartet group of *Crepidula* has doubtless the same effect of lessening the external area of the quartet in that region, while the neighboring third quartet cells would lie relatively higher in this form than in *Fiona*. So when the second velar row forms in *Crepidula* it will lie relatively lower in the second quartet group ($2b^{22}$) and more probably involve third quartet cells, as Conklin states it probably does.

Regarding the lineage of the velum of *Planorbis*, Holmes says that "the tip cell (of the anterior arm) divides as far as I can determine, but once, and the two daughter cells become pushed apart by the cell $1b^{1211}$, which forms the median cell of the upper row. These cells extend to the anterior trochoblasts on either side, but in later stages they may sometimes be separated from them by cells which wedge in from below". The anterior trochoblasts follow these cells posteriorly, but Holmes states that the tip cells of the lateral arms "do not form a part of the prototroch but enter into the formation of the head vesicle". In this *Planorbis* differs from *Fiona*. Blochmann states that the right and left tip cells enter the velum of *Neritina*. The lower cells in the prototroch Holmes derives from the second

quartet, though he adds that at a later period cells are joined to the prototroch from below, the lineage of which is obscure.

In *Ischnochiton*, the larva of which is, in its velar aspects, remarkably like the trochophore of Annelids, Heath finds that the prototroch is composed of trochoblasts, of "accessory trochoblasts" (derived from the original basal cells of the molluscan or intermediate girdle cells of the annelidan cross) of the tip cells in the anterior and lateral arms, while in the posterior arm the tip cells go into the ventral plate, the gap in the trochal ring being there bridged by derivatives of the median cell of that arm of the cross. Thus in this annelid-like form of larva none but derivatives of $2a^{11}$, $2b^{11}$ and $2c^{11}$ from the second quartet form the trochal ring.

The prototroch of *Trochus* (Robert) is composed of twenty-five cells, sixteen of which comprise the trochoblasts, six represent the divided tip cells of A, B and C quadrants, while the other three are the cells 2a, b, c^{12111}. A very exact and close comparison may here be made with the prototroch of the Annelids *Amphitrite, Arenicola* and *Clymenella*, particularly with the former, for, as Robert says, "Vingt-deux ont indetiquement la même origine et la même disposition que celles de *Amphitrite;* le trois autres (2a, b and c^{12111}) sont des derives des cellules correspondantes de la même *Annelide.*"

Among Annelids Wilson has found that the prototroch of *Nereis* arises entirely from twelve of the sixteen primary trochoblasts, there being no contribution from the second quartet. All sixteen of the primary trochoblasts enter the prototroch of *Amphitrite* and *Clymenella* (Mead), as is also the case with *Arenicola* (Child) and *Podarke* (Treadwell). Regarding the close resemblance between the trochophore of *Ischnochiton* and those of the Annelids, Heath says: "The origin, development and fate of these cells (primary trochoblasts) is precisely similar to the primary trochoblasts in *Ischnochiton.* The second quartet in *Amphitrite, Clymenella* and *Arenicola* furnishes three cells in each quadrant except the posterior, which enter the prototroch. Two of the three are homologues of the divided tip in *Ischnochiton,* while the third corresponds to a post-trochal cell".

If now we compare the derivation and ultimate structure of the annelidan prototroch with the typical molluscan velum some interesting causal relations appear. At the time of its functional activity the prototroch of Annelids is apparently a radially symmetrical structure. Among the Mollusks we find, as a rule, a velum strongly developed anteriorly, with a considerable area of weakly ciliated ectoderm between the ends of its posterior arms. There are numerous excep-

tions to this typical molluscan velum, *Ischnochiton* and *Trochus* for examples, in which the trochal ring is as complete as among the Annelids. Returning now to the developmental history of the two groups certain variations are found which, when viewed in the light of functional larval structure, appear as a natural result of the divergent forms of the larvæ, these variations having been precociously thrown backward upon the cleaving cells of the ovum. In *Amphitrite*, *Arenicola* and *Clymenella* among the Annelids, and *Ischnochiton* and *Trochus* representing the more primitive Mollusks, all the primary trochoblasts ($1a^{211}$, ^{212}, ^{221}, ^{222}, etc.) in all quadrants go into the prototroch, while in *Nereis* the same occurs with the exception of four, which may for all four quadrants be designated $1a^{221}$; these are not functional in this manner, but are pushed inward and form part of the cephalic vesicle. In *Crepidula* only the anterior trochoblasts help form the preoral velum ($1a^{22}$, $1a^{21}$, $1b^{22}$, $1b^{21}$), and the same is true of *Planorbis* and possibly also of *Fiona*. Accessory trochoblasts ($1a^{1221}$, $1a^{1222}$, etc.) form a part of the prototroch of *Ischnochiton* in all quadrants, while in *Podarke* the cells $1a^{1222}$, $1b^{1222}$, $1c^{1222}$, corresponding to three of the above series, aid in the formation of the prototroch ("secondary trochoblasts" of Treadwell). In *Planorbis* Holmes finds that the cell $1b^{1211}$ is the "anterior median" cell of the prototroch, but does not find similar conditions in any other quadrants. None of these elements which are, of course, derivatives of the annelidan outer intermediate or molluscan middle cells (with the exception of $1b^{1211}$ of *Planorbis*, which comes from the inner basal) are found in the antero-lateral portion of the prototroch of *Amphitrite*, *Arenicola*, *Clymenella* and *Nereis*. In all the above forms except *Nereis* elements from the second quartet are also added to the prototroch, and these may be designated with Treadwell "tertiary trochoblasts". In *Amphitrite*, *Arenicola* and *Clymenella* the prototroch is increased in A, B and C quadrants by the cells $2a^{111}$, $2a^{112}$, $2a^{121}$, etc. In *Podarke* $2a^{112}$ and $2a^{121}$ in A quadrant, and similar cells in B and C, function in like manner, while *Ischnochiton* shows the same, for $2a^{111}$, $2a^{112}$, etc., enter the prototroch from the anterior and lateral quadrants ("secondary trochoblasts" of Heath). Of *Hydroides* Treadwell says: "Cells are added from the lower hemisphere". For the prototroch of *Trochus* Robert derives the three cells from the second quartet in A, B and C quadrants ($2a^{111}$, $2a^{112}$, $2a^{12111}$, etc.). Coming to those Mollusks which possess a typical veliger, more cells are found to be contributed by the second quartet, particularly in the anterior quadrants. In *Crepidula* the tip cells of the anterior and lateral arms go into the first velar row, while below numerous cells are

added, so that the second row contains "probably a few cells of the first, many of the second and possibly a few of the third quartet". The velum of *Planorbis* is rudimentary in structure but shows the same general type of development as *Crepidula*, and here in like manner second quartet cells are added. The tip cells of the lateral arms, according to Holmes, do not enter the prototroch, but cells of the same series below them function in this manner. In the anterior region both tip cells and those lying beneath them from the second quartet enter into the prototroch.

From this short comparison of the lineage of the trochal area in Annelids and Mollusks, it will be seen that as in the functional larval form the typical molluscan velum shows greater anterior development than the prototroch of Annelids, so also cells taken from the segmented egg to complete the velum in this region exceed in number those destined to form a similar area of the annelidan trochophore. To do this the second quartet has become greatly encroached upon in furnishing necessary building material for this structure in those Mollusks whose larvæ show strong anterior velar development, and in *Crepidula* the third quartet also possibly becomes involved. It is natural to conclude, as indeed the facts show, that those Mollusks which in the structure of their larval prototrochs show great similarity to the homologous structure of the Annelid trochophore, will exhibit a similar lineage of the cells constituting the larval organs compared—examples, *Ischnochiton* and *Trochus*.

Later Velar Development.—With continued invagination of the stomodæum and constriction of the foot, the velar area, which has thus far been marked only by an irregular double row of cells extending around the anterior half of the head vesicle and losing itself in the posterior portion of that larval organ, becomes more prominent and takes on the bilobed outline so characteristic of the anterior end of veliger larvæ. At first the velar lobes are merely rounded swellings gradually rising from the upper sides of the head vesicle and curving around, downward and inward toward the stomodæum (fig. 105). The cells in this region do not as yet exhibit that differentiation which later marks the prominent ciliated margin from the underlying region. But as the lobes begin to constrict beneath and become more prominent (fig. 106), those cells which lie on their most peripheral surface show marked increase in size, and the ciliation which hitherto has been uniform and weakly developed becomes more prominent in these cells. They may now

be observed lying in a row on the rounded edge of the expanding ridge, and though at first this series of cells is indistinctly marked, it continues to increase in definiteness and in the size of its component elements. Figs. 106, 107 and 108 (Pl. XXXV) show successive stages in the elaboration of these large heavily ciliated cells of the velar edge, and sections, as figs. 91 and 92 (Pl. XXXII) in particular, show the great increase in size which now marks them.

Coincidently occurs the expansion of the velar lobes to form the broad wings or velar folds which characterize the functional larva at the time it becomes free-swimming. As the velar area expands it becomes deeply notched below where the lobes of the opposite side rise to meet over the mouth, and this growth in length and breadth is marked on the dorsal side as well. Figs. 109 and 110, side and dorsal views of the same veliger, show the condition of development of the velum just before the larva breaks from the egg capsule, though in these drawings from fixed material the velum is of necessity considerably contracted. In fig. 110 it will also be noted that the region just above the mouth has grown out into a projecting process, and it is upon this area that the former apical point (animal pole) lies.

Head Vesicle.

The Head Vesicle of *Fiona* reaches its greatest prominence at a stage shown in fig. 104 and slightly older larvæ. Somewhat later (figs. 105, 106) it becomes actually larger, but relatively smaller when compared with the larva as a whole, and has also become greatly involved in the formation of the velar lobes. It is composed of cells of the first quartet lying within the trochoblasts and ends of the arms of the cross, and its greatest extent is covered by cells which lie posterior to the lateral arms. A posterior cell plate, such as is found in *Crepidula*, is not here developed, for though doubtless the same cells are present, they have multiplied to a much greater extent than in *Crepidula* or *Planorbis*, and form a layer of small cells which are scarcely distinguishable from those in front or at their sides. Neither is an apical cell plate demarkated in the region corresponding to the location of that structure in *Crepidula*, the cells in front of the apex being all of similar size and seemingly without regularity of arrangement, so that it is with the greatest difficulty that the apex can be located among the large number of small cells of equal size by which it is surrounded. As has been described before, the point of greatest forward extension lies first in the region of the tip of the anterior arm of the cross, but with continued growth the apical area becomes pushed forward so that it shortly occu-

pies the point of greatest anterior extension, while the tip region of the anterior arm through which the velum runs lies ventral to the apex in the direction of the blastopore (figs. 95, 98). At the same time the head end becomes rounded by increased growth of the cephalic area.

The four original apical cells, as shown in figs. 75 and 76, divide soon after and again at a stage represented by fig. 95, so that this region, which in *Crepidula* is in the fully developed veliger still marked by four apicals ($1a^{1111}$, etc.), here comes to consist of at least twelve very small cells, among which no regularity of arrangement is sufficiently marked to be of value in orientation. These cells are extremely difficult to distinguish from numerous other cells of like form and structure which cover the anterior surface of the head vesicle. The apical group continues its forward migration in relation to the larva as a whole and, as it appears, pushes aside some of the cells which have arisen from divisions of the inner and outer basals of the anterior arm, for at a later period (fig. 108) the apical group lies close against the first velar row. Either such a shifting occurs or the basals become involved in the development of the velum. In fig. 108 a row of cells may be distinctly observed in which the nuclei are particularly large, extending laterally from the apical point. My first thought on seeing them was that they were a part of the velum, but after definitely locating the position of the apex and following the later history of the velum, it is clearly seen that this row never enters into the latter structure, but represents in its cell-lineage derivatives of cells of the lateral arms of the cross. No ciliation has been discovered in the apical area, and such structures are certainly not strongly marked, though without examining living material a denial of the possible presence of such structures would scarcely be conclusive.

Nerve and Sense Organs.

Cerebral Ganglia.—The cerebral ganglia arise at a stage about corresponding to fig. 105, though they do not become well marked until somewhat later (fig. 108). During this period cells may be seen proliferating inward from the ectoderm of the head vesicle in the two regions which lie lateral from the apical area. A row of cells with large nuclei are at this time plainly visible running laterally from the apex, and it is along the anterior side of these cells that the ganglia first arise. This row has been identified as coming from the lateral arms of the cross, and cells lying between it and the anterior portion of the first velar row are from the same source.

Later many of these large cells also divide and go into the ganglia. Thus it will be seen that the two cerebral ganglia arise from elements of the two lateral arms, the anterior rosettes, and probably also from some cells of the anterior arm which have been pushed laterally by the advance of the apex and lie in the region where the ganglia develop. The tip cells of the lateral arms certainly do not take part in the formation of the ganglia, as they lie too far laterally and probably go into the velum. Where no large cells, the definite lineage of which is known, are left as landmarks, it is obviously impossible to give absolute derivatives for the ganglionic rudiments. Comparing, however, the above approximate derivation with other Mollusks which have been studied in this connection similarities are evident. In *Crepidula* the ganglia "very probably arise from the lateral extensions of the anterior arms". Holmes has been able to state very definitely the manner of origin of these ganglia in *Planorbis*, as here they are surrounded by conspicuous cells. He says: "The tip cells of the lateral arms and the cells lying immediately above them do not enter into the formation of these masses; with the exception of these, two cells in each arm, all the cells in the lateral arms of the cross, the cells of the anterior arm, except the tip and basal cell, and the central region of the cross, except the four apicals, and the two cells lying in front of them, enter into the formation of these rudiments".

Otocysts and Pedal Ganglia.—The otocysts appear at a considerably earlier period than the ganglia which innervate them or the cerebral ganglia. They are first seen as slight invaginations on the sides of the foot slightly below the stomodæal invagination, and at a stage shown in figs. 103 and 104 have developed to deep pits, the openings of which have become much constricted. As these constrictions narrow, the two otic vesicles arise and are connected with the external ectoderm by strands of cells which resulted from the constriction of the outer portion of the invaginations. Somewhat later the pedal ganglia are seen slightly external to the otocysts in position. These ganglia arise in part from the strands which connected the otocysts with the ectoderm, and in part from other cells proliferated from the ectoderm in the same region. At first the cerebral ganglia are not connected with each other by a commissure nor with the pedal ganglia, but later cells grow out and meeting connect the cerebral ganglia together, while between cerebral and pedal ganglia like connectives arise, probably both ganglia contributing cells to their formation. These connectives are very large (fig. 94),

and the whole cephalic nervous system is much concentrated. Behind the pedal ganglia and somewhat higher dorsally may be distinguished, particularly in older larvæ, the rudiments of the pleural ganglia, which also appear to have arisen by delamination of the ectoderm and lie in close association with cerebral and pedal ganglia. A very heavy commissural strand connects the two pedal ganglia, and the whole nervous system of the larva foreshadows in its compact structure the adult condition, individual ganglia being difficult to distinguish. Figs. 92 and 94 show sections through this region at a somewhat later period than figs. 88 and 89. Eyes have not developed to a functional condition in the oldest larvæ observed. Sections of these show pigment granules within cells lying close to the cerebral ganglia, and in some cases these cells lie around a slight invagination of the ectoderm—the first evidence of optic organs.

Excretory Organs.

The large excretory cell which lies on the right side of the larva and forms the chief member of a group of similar greatly vacuolated cells lying in that region arises from the third quartet in the C quadrant, and from its large size and conspicuous appearance its complete history is known. Returning to a segmentation stage, in which the egg contains about one hundred and twenty cells (fig. 70), it will be seen that the third quartet group in C quadrant contains seven cells. Divisions next occur in the three large cells, $3c^{1212}$, $3c^{1112}$ and $3c^{1211}$ (fig. 77). The cell $3c^{1111}$ does not divide with these, nor does it ever again divide, but continues its growth, soon becoming the largest element in the ectoderm. As gastrulation proceeds this large cell, $3c^{1111}$ (Ex.), the origin of which is thus established, appears at the right of the elongating gastrula (left of figs. 78,, 79) and with the closure of the blastopore lies midway between dorsal and ventral surfaces, as shown in figs. 98 and 99. It has become much larger, when compared with its neighboring cells, both from lack of division and by actual growth. As the veliger takes form this cell becomes yet more marked (fig. 102), and when the shell gland has become prominent (fig. 104) it is seen lying in a slight depression surrounded by small cells which are in an active state of division. As the foot arises and the cephalic end of the veliger is differentiated from the body, the large excretory cells move upward along the body just posterior to the pedal groove, on the right side, this change of position being a natural sequence of the general torsion of that region (figs. 105, 106). The intestine has also become well developed by this time as a solid strand of cells connecting the pos-

terior end of the enteric cavity with the ectoderm, and this latter point of contact is just below the large excretory cell. Fig. 88 shows a section through this region, showing the excretory cell to be much vacuolated and to lie for the most part below the ectoderm. At a considerably later stage (figs. 109, 110) its position and structure are shown just before the veliger escapes from the egg capsule. A large nucleus, which usually contains several small nucleoli and having the general appearance of nuclei in cells which have for a long time remained undivided, lies at the lower end of the cell. The cytoplasm is greatly vacuolated and at its peripheral end, where it meets the exterior, is seen a deep pit with constricted mouth. This appears to function as an intra-cellular duct, for it comes into connection at its inner end with the large vacuoles which fill the cell. Just above and anterior to the large cell is a group of smaller ones which contain darkly stained nuclei and pigment granules. One of these, the largest, also contains vacuoles and lies nearest the cell $3c^{1111}$. In somewhat older larvæ one or two of these smaller cells, which lie close to $3c^{1111}$, have increased much in size, become greatly vacuolated and appear to function as their larger neighboring cell. These smaller accessory excretory cells are also doubtless of ectodermal origin and, since they lie between the principal one and the blastopore, are doubtless derived from the same quartet.

In addition to the excretory cells above described others of a similar nature are found in the larva of *Fiona*. Sections (figs. 90, 91) of fairly well-developed veligers show two cells (Nph) nearly symmetrically placed on the two sides of the body just behind the constriction separating head from body region. These cells contain large nuclei and their protoplasm is clear and greatly vacuolated. In a slightly older stage (the oldest larvæ examined) yellowish-brown granules are very evident, lying in the meshwork of the vacuolated cytoplasm. The cell on the left side (fig. 91) lies just to the side of and slightly higher than the otocyst of that side, being closely associated with its ganglia, while the one on the right side (fig. 90) lies higher and is in close proximity to the smallest cells of the large excretory organ of that side. It may be distinguished from the cells of this organ by its clear cytoplasm and the color of the granules lying in it. In later stages another cell of similar nature may be seen beside the one on the right side, but only one has been observed on the left. The origin of these cells is not known. In earlier stages cells of slightly smaller size lie in the regions which they later occupy, but cannot be distinguished in structure from neighboring mesodermal elements. However they lie close to

the ectoderm and may have come from that source. The later fate of these cells is unknown, but as they are increasing in size they probably function as important larval organs. They will here be designated "nephrocysts," for they correspond to cells of similar position and structure described by Trinchese (1881) for the larva of *Ercolania* and other Nudibranchs, by whom an excretory function was ascribed them. Older and living material is desirable before making definite statements regarding the nature and function of these apparently similar larval organs of *Fiona*.

Numerous investigators have seen and described with various interpretations the excretory organs of larval Opisthobranchs. As early as 1839 Lovén observed the anal kidney in Nudibranch larvæ, but did not recognize its function, though indicating that it was probably an undeveloped sexual organ. Likewise Sars (1840) described a similar structure in the veliger of *Tritonia*, which, together with the large endodermal cell which lies near it, he associated in common function with the liver lying on the opposite side of the enteron. In *Æolis* like structures were found. Later (1845) he distinguished the vacuolated excretory cell and its neighboring pigmented cells, classing the whole as a reproductive anlage. Reid (1846) observed a like structure in a number of Nudibranchs (*Doris*, *Polycera*, *Doto*, etc.), considering it to be probably the heart from contractions which he saw it undergo. In Vogt's very thorough paper on *Actæon*, appearing in 1846, the excretory organ is somewhat neglected, though his figures indicate its presence. Nordman in the same year described this organ in *Tergipes*, and referred a reproductive significance to it. Schneider (1858) also found it in *Phyllirhöe*, but assigned no definite function. Langerhans (1873), having observed in the living larvæ of *Doris* and *Acera* cells in the anal region which contained concretions, and from which drops were extruded considered the organ to be of an excretory nature. In 1875 Lankester found similar conditions in *Aplysia*, and considered the organ to have arisen either from intestinal cells near which it lay or from the ectoderm.

Trinchese (1881) described an "anal gland for *Ercolania* which is strongly pigmented and lies on the right side of the body". This he believed arises from three or four mesodermal cells which acquire pigment and by their division form the organ in question. The same was found in *Amphorina*, *Bergia* and *Doto*, in the last case being paired. In addition to the anal excretory organ, Trinchese also found in the above forms two "rini primive" in the dorsal region under the ectoderm, one right and the other left. These he described as vesicular,

spherical or ovoid bodies having a lower part full of transparent liquid, in which lay concretions of a yellowish color. These he denominated "nephrocisti" (nephrocysts) and ascribed to them a mesodermal origin, since they have no connection with the exterior. Haddon (1882) found a mass of cells on the right side of *Jantheria* and *Philine*, near the anus in *Elysia* on the left side, and in *Pleurobranchidium* on both sides. In 1888 Rho found similar organs in *Chromodoris* which he stated arise from a few mesoderm cells containing numerous concretions and excreta which indicate their functional value. He concluded that this structure corresponds to the right Prosobranch kidney, considering the left to be rudimentary. Lacaze-Duthiers and Pruvot (1887), in a paper on Opisthobranch embryology, described the anal organ of *Aplysia*, *Philine*, *Bulla*, *Pleurobranchus*, *Doris* and members of the family Æolididæ, stating that in origin it is entirely ectodermal and that it was none other than an "anal eye." This eye, it was claimed, becomes strongly developed in the blind larvæ and later atrophies as true eyes appear. It stands in connection with a cell-mass, ganglionic in nature, the "asymmetrical centrum" of Lacaze-Duthiers.

Mazzarelli (1892) came to some very different conclusions from work on *Aplysia*. He believes the organ in question to have neither the structure nor function of an eye, and, moreover, it remains present in the larvæ after eyes are developed. From its position and structure it is doubtless a kidney. He derives it from paired rudiments which originally were closely associated with the endodermal elements of the aboral pole (mesentodermal cells) and which later, separating, wander into the blastocoel cavity and, after torsion begins, first the left and then the right come to lie in the neighborhood of the anus and together form a small cavity which acquires communication with the exterior. This unpaired kidney is homologous to the kidney ("niere") which in many Prosobranchs is found in the same place and, as is well known, forms the anlage of the definitive kidney. Mazzarelli, therefore, concludes that the anal kidney of the Opisthobranch larva is a secondary kidney ("secondare niere"), while the primitive kidney of these Mollusks is already known (the "nephrocisti" of Trinchese). The anal kidney is but the anlage of the definitive kidney, which in this case corresponds not to the right but to the left adult kidney of the Prosobranch.

Heymons (1893) has carefully described the conditions found in *Umbrella*. The excretory rudiment is here at first paired and arises from the cells $3c^{11}$, $3d^{11}$, which sink somewhat below the surface and

divide several times, one cell in each group remaining large. Thus the excretory cells of *Umbrella* are ectodermal in origin. In further history Heymons finds that the large cell of the left side decreases in prominence and finally is indistinguishable from those surrounding it, while the right continues to enlarge and, with the torsion of the larva, is carried higher on that side. Later a second large cell appears by the side of this one, which Heymons thinks cannot represent the original left cell, as this would presuppose too great a migration, but rather one of those associated with the original right, the growth of which has been delayed. The function of a larval excretory organ is assigned only to this group of cells by Heymons.

In 1895 Mazzarelli, after a study of the development of a large number of forms (*Philine, Gastropteron, Actæon, Oscanius, Pleurobranchus, Tethys, Archidoris, Aplysia, Hermæa, Janus, Polycera* and *Haminea*), came to the conclusion that the anal organ of Lovén, Sars, Pruvot, Lacaze-Duthiers and others was not, as Lacaze-Duthiers, Pruvot and Heymons maintained, of ectodermal origin, but rather mesodermal, arising from two large and other smaller mesoderm cells which become pigmented and which by a slight ectodermal invagination acquire an external opening. In later development he finds these cells form a connection with the pericardium, which has arisen from a mesodermal mass closely connected with them. Therefore, he concludes that the anal kidney of the Opisthobranch larva is not homologous with the head kidney of the Prosobranchs, but from its origin, position and relation (particularly in connection with the pericardium) it is none other than the anlage of the definitive kidney of the adult And also, since it lies to the left of the rectum, it corresponds to the kidney of the Gastropods which possess but one, and to the left kidney of those with two. Viguier (1898) describes the anal kidney of *Tethys*, distinguishing an excretory lumen, around which are grouped several cells; he does not indicate its origin.

Among the Prosobranchs externally situated larval excretory organs appear to have been found generally. Salensky (1872) has described such bodies filled with concretions lying upon the side of the body in *Calyptræa* and *Nassa*. Bobretzky (1877) found the same in *Fusus*, these cells lying behind the velum and without an underlying ectodermal layer. This latter condition is placed in doubt by McMurrich (1886). Similar organs to the above were found in *Fissurella* by Boutan (1885), while in *Capulus* (v. Erlanger, 1893) a single large ectodermal cell, probably excretory in function, was found on each side of the body behind the velum. For *Crepidula* Conklin (1897) has

minutely described a group of ectodermal cells lying laterally just behind the velum and probably arising from the second quartet; they become much vacuolated, filled with darkly stained granules and before metamorphosis separate from the ectoderm and are lost. Erlanger (1892) concluded that the larval kidney of *Bythinia* was partly ectodermal and partly mesodermal, and had no connection with the definitive kidney of the adult. The earlier results of Bütschli (1877) on *Paludina* as well as *Bythinia* were enlarged by Erlanger (1891–2), showing that in these fresh-water Prosobranchs the larval kidney was formed from inner mesodermal and outer ectodermal portions.

Rabl (1879) established a mesodermal origin for the primitive kidney of *Planorbis*, and Holmes (1900) in his late work confirms the same. Fol (1879) derived the larval kidney of *Planorbis* entirely from the ectoderm. Wolfson (1880) described the larval kidney of *Limnæa* as arising from a large velar cell on either side which migrates inward, retaining connection with the exterior through an intra-cellular duct. Meissenheimer (1898) says of *Limax*, we have "in der urniere ein rein ekto-dermales Gebilde vor uns, zu dem das Mesoderm auch nicht den geringsten Beitrag geliefert hat." From his figures and discussion it appears very evident that in this form the primitive kidney is purely ectodermal in origin. In 1899 Meissenheimer published his investigations on the "Urniere der Pulmonaten" (of the Basommatophora, *Ancylus, Physa, Planorbis, Limnæa,* and of the Stylommatophora, *Succinea, Helix, Arion, Limax*). In both these groups he shows the larval kidney to be entirely ectodermal in origin and similar in structure, the urinary tube of the latter group being many-celled, while in the former but four cells comprise it. In both a ciliated cell or cells closes the inner end of the tube, and for this reason Meissenheimer compares the primitive kidney of the Pulmonate with the end cells of the water vascular system of the Platyhelminthes.

Among the Lamellibranchs Hatschek (1880) describes the larval kidney of *Teredo* as probably both ecto- and mesodermal in origin. In the single left primitive kidney of *Cyclas*, Stauffacher (1897) found a similar though more complicated structure arising from both ectodermal and mesodermal elements.

Meissenheimer (1901) finds that in *Dreissensia polymorpha* the larval kidneys arise from ectodermal cells wholly, each of the two being formed from a few in-wandering cells. The structure is more simple than that of the Pulmonates and Meissenheimer suggests that it may be the ground type of the group. This might then be described as an ecto-

dermal invaginating tube with the end closed by a vacuolated heavily ciliated cell.

From the above account of some of the more important observations and conclusions upon the nature and origin of the larval excretory organs of the Lamellibranchs and Gastropods (and of the latter more particularly of the Opisthobranchs), one is strongly impressed with the feeling that much more work must be done upon these organs of mulluscan larvæ before we are ready to come to definite conclusions regarding their mutual relations and homologies, if such exist. Nor has the investigation recorded in this paper brought forward facts which justify an immediate solution of the problem. The anal kidney of *Fiona* doubtless corresponds to the similar structure described for so many members of the Opisthobranchia, but its derivation is totally different from the results obtained by some of the more recent and careful workers in this group.

Mazzarelli's conclusions regarding its mesodermal origin, resulting from investigations upon a large number of closely related forms, are very different from mine. There is no point regarding the cytogeny of *Fiona* of which I am more certain than that the group of cells constituting the anal kidney is of ectodermal origin, and one member of the group (the largest, $3c^{1111}$) has been traced through every step of its history, from the initial cleavages which produce it to its functional condition upon the right side of the veliger larva at the time of hatching. In this respect my results are entirely in accord with those of Heymons for *Umbrella* and, except for the function assigned to the resulting organ, agree closely with Lacaze-Duthiers and Pruvot's derivation of the same structure from ectodermal cells. With regard to the fate of this organ, the work of Rho and Mazzarelli appears to show conclusively that it becomes metamorphosed into the kidney of the adult, and the latter's comparison of this organ with the adult kidney of those Gastropods which possess but one, or with the left of those with two, is in entire accord with the generally accepted opinion upon this subject. Unfortunately material has not been available for a study of the metamorphosis of *Fiona*. But on *à priori* grounds it should be similar in all essential features to the above-mentioned processes of development in closely allied forms. The metamorphosis of the anal kidney of the larval Opisthobranch into the definitive kidney of the adult might seem, at first sight, fair grounds on which to doubt its ectodermal origin, since the latter structure has generally been considered to be a mesodermal derivative. But if in this connection be considered the recent results of Meissenheimer, who derives the adult

kidney and allied structures of *Limax* and *Dreissensia*, representing two distinct molluscan groups, from ectodermal rudiments, after an investigation which bears every evidence of care and accuracy, the possibility at least of a similar manner of formation among the Opisthobranchs must be granted.

So little is as yet known of the "Nephrocysts" of Trinchese that any discussion of their significance and possible homologies must of necessity be largely hypothetical. An exact knowledge of their derivation and structure would be of the utmost value. In *Fiona* when first seen they lie in the cleavage cavity, but whether they have wandered there from the ectoderm or are from the first mesodermal in character is yet an unsolved problem. Should they prove to be of ectodermal origin their position might justify a close homology with the Prosobranch larval kidney, and possibly also with those of the Pulmonates and Lamellibranchs, since Meissenheimer has indicated the larval kidneys of the two latter groups to be of ectodermal origin, and his work is supported by the earlier investigations of Wolfson and Fol. Should these nephrocysts prove entirely mesodermal there is yet a possibility of their similarity to the larval kidneys of the Prosobranchs, Lamellibranchs and Pulmonates, through the investigations of Bütschli and Erlanger for the Prosobranchs, Rabl and Holmes for the Pulmonates and Hatschek for the Lamellibranchs, who derived the primitive kidney of members of these groups in part or entirely from mesodermal elements. However, the structure of the nephrocysts of Opisthobranchs is very different from the primitive renal organs of the groups above cited, for, as far as is known, they appear wholly enclosed in the schizocoel with no external ducts. The fact of their very rudimentary structure suggests an explanation for the great development reached by the anal kidney. When we consider that in other groups possessing true larval excretory organs the anlage of the definitive kidney does not develop into a condition of functional activity until after metamorphosis, while among Opisthobranch larvæ, even before the time of hatching, certain cells of this structure are actively concerned in the work of excretion, the causal relation between rudimentary structures on the one hand and advanced development on the other is brought forcibly to mind. The nephrocyst of the Opisthobranch is not a prominent or well-developed structure, and with its phylogenetic decline precocious development has arisen in the rudiment of the definitive kidney, resulting in functional activity in a part at least of its formative elements long before development of the adult organ.

There is yet another possible explanation of the renal organs as found in Opisthobranch larvæ which will be stated but briefly, since a preponderance of hypothesis over fact is always to be regretted. It is generally conceded that whether the anal kidney be of mesodermal or ectodermal origin its rudiment is at first a paired structure, one part of which may fail to develop into a renal organ (Heymons) or unite with the other (Mazzarelli). The nephrocysts are paired structures, one lying close to the anal kidney, the other in an almost similar position on the opposite side of the body. It is possible that the nephrocyst of the right side is but a part of the anal kidney of that side, while that of the left represents the degenerate whole of the rudiment of that side. In this case, of course, true larval kidneys would be wanting.

The Enteron.

As the archenteron arises from the cleaving entoblast it presents, when viewed from the vegetative pole, an irregular depression, the bottom of which lies considerably below the edge of the blastopore. The macromeres, 5A, 5B, 5C and 4D, are at the bottom of this pit, with 5a, 5b and 5c lying peripherally from them, while above these and next to the ectoblast come $4c^2$, $4b^2$, $4a^2$ and the smaller cells $4c^1$, $4b^1$ and $4a^1$. In the posterior region are found the small cells E^1, E^2, e^1, e^2 (enteroblasts) which have arisen from 4d. The fifth quartet and all the macromeres are the next cells to divide, this resulting in enlargement of the wall area of the enteron, and by this division into smaller elements closer contact between the blastomeres results. Hitherto the entoblasts have been much rounded (except those meeting directly in the center), and have lain together in a very irregular manner, particularly after invagination began. With diminution in size and rearrangement of these cells a distinct cavity with closed dorsal wall arises (fig. 80). At the anterior end lies the large cell $4b^2$, while posteriorly and laterally are found the two large cells $4a^2$, $4c^2$; between and behind them are the enteroblasts. At first the enteron is longer on the right side (left of figures), the cell $4c^2$ lying more posterior than $4a^2$, this being the natural result of the division which early separated the large mesentomere from 4D of that side and the lack of growth and division in this latter cell for so long a period. But as development proceeds and the whole enteron grows in antero-posterior extent it will be noted that $4a^2$, which is a very large cell and easily distinguishable, gains in its backward course upon the opposite cell of like lineage ($4c^2$), comes to lie opposite to it and later more posterior (figs. 80, 81, 82). This process is the beginning of the torsion of the intestine, and is appa-

rently to be explained in at least its first manifestations as the direct result of increase in growth of one side over the other. After $4a^2$ lies considerably more posterior than the derivatives of the large cell, which before lay opposite it ($4c^{21}$, $4c^{22}$, fig. 81), the cell $4b^2$ is seen to be undivided as yet and still at the anterior median point of the enteron, showing that the change of position of $4c^2$ relative to its opposite cell has been the result of greater increase in the area of the left over that of the right enteric wall.

During this process $4a^2$ has not been observed to divide and it maintains its large size throughout. On the opposite side $4c^2$ has divided into cells of equal size and divisions are continued in this region, resulting in the thinning of that portion of the enteric wall and an equalization of the size of the cells which compose it. With the continued growth of the enteron $4a^2$ is moved still more posteriorly and finally toward the right (left of figs. 82, 83). In fig. 84, which represents the enteron in optical section at a stage about corresponding to fig. 104, $4a^2$ is seen lying directly in the median line. Above, in the anterior median portion of the enteron, is a group of large yolk-ladened cells which have been derived from $4b^2$ and its neighboring cells. This group will soon shift somewhat to the left and become the rudiment of the liver.

As was seen before, the small cells E^1, E^2, e^1, e^2, which were separated from the anterior end of the mesentoderm, at first lie between $4a^2$ and $4c^2$. An actual section at this stage parallel to the ventral surface (fig. 85) shows that the inner of these cells are yet in contact with the enteric cavity. I am confident that the cells in this figure marked "enteroblasts" represent mesentoblastic derivatives. Their history, position, size and the structure of their nuclei, which are small and darkly stained, correspond to these cells. With the increase in extent of the left side of the enteron and, after the closure of the blastopore, by its continued growth, these enteroblasts, which may be distinguished from their neighbors by their darkly staining nuclei and their smaller size, become pushed from the median plane toward the right side as the large cell $4a^2$ advances around to a more and more posterior position (fig. 83). Finally, when $4a^2$ itself lies on the median line, these cells lie entirely to the right and are more posterior than those which have come from 4c and 5c. A slightly diagonal actual section, as fig. 86, shows the large cell $4a^2$ in the median plane. Just behind it and slightly to the right are shown in the section five small cells lying closely pressed between $4a^2$ and the shell-gland invagination behind. These cells correspond in position and in appearance to the small enteroblasts

of fig. 85. If we now examine section fig. 87, which is taken through a veliger slightly older than that shown in fig. 104, the relation of the enteron to its surrounding structures may be observed. The large entodermic cell, $4a^2$, has been successively traced through preceding stages from its origin on the left side of the archenteron to its final position on the right of the enteric cavity, as is shown in the figure. Just posterior to this will be noted a mass of cells connecting the enteron with the ectoderm. The nuclei of these cells are compact and deeply staining, and the cytoplasm is decidedly clearer and contains less yolk than that of the cells directly surrounding the enteric cavity. Moreover, their position beside the large cell $4a^2$ and now, through the torsion which the enteron has undergone, their later position somewhat posterior to this cell, indicates the probability of their correspondence with the "enteroblasts" of fig. 86 (Pl. XXXI) and earlier stages, in which the identity of these cells is unquestioned.

It is proper in this place to consider again the results of Carazzi's work on *Aplysia* and its relation to the mesentodermal history of *Fiona*. It will be remembered that Carazzi's account of the lineage of 4d up to a stage when its derivatives number twelve cells exactly parallels my results on *Fiona*, but regarding the fate of these cells there is lack of agreement. The anterior small cells of *Aplysia* are believed to be purely mesoblastic, while at least four of them in *Fiona* appear, from the preceding account, to be entodermal in nature. Carazzi, however, derives endoderm from the two small posteriorly directed cells (e, e^1 of *Aplysia*) which correspond to z^1, z^2 of *Fiona*. These latter cells were last seen lying at the posterior end of the gastrula of *Fiona* closely pressed against the ectoderm. At a later period, when a large number of mesodermal elements lie in this region, the z^1, z^2 cells become indistinguishable from these. Sections of later stages (fig. 87) show two cells which are larger and clearer than the enteroblasts and which lie against the ectoderm where the intestinal mass touches it. They may represent the cells z^1, z^2, but of this there is no evidence except that given above. Anal cells are not a marked feature of the developing embryo of *Fiona*, but at this time sections in particular show two cells of somewhat larger size than the surrounding ectodermal elements, against which the forming intestine abuts and which are doubtless comparable to the anal cells of other forms (fig. 87, An.C).

It will now be seen that the portion of the enteron lying most posterior and close against the shell-gland invagination has been derived from the cells which formed the bottom and the left side of

the original archenteric invagination (5B, 5b, 4C, 5C, 5c, 4D, 5A) while dorsally and anteriorly are seen more yolk-ladened elements whose origin may be traced to the large entoderm cell $4b^2$ and those around it. The stomodæal invagination breaks through at a much later period between the descendants of 5a and 4b and their neighboring cells, which have been turned in an anterior direction, while doubtless cells from 4c and 5b also push in upon this region with the closure of the blastopore. By the torsion which the enteron has undergone the upper mass of large yolk-ladened cells is moved more and more to the left, while in like manner $4a^2$ turns to the right. While this is occurring the invaginating shell-gland has pushed the anterior and posterior walls of the enteron very closely together, both enteric and cleavage cavities being practically obliterated (fig. 86). When this structure evaginates the enteron again opens out and has then lost its elongated form, being rounded with its wall cells in close contact (fig. 87).

In *Umbrella* as well as in *Fiona* $4b^2$ occupies the anterior end of the enteric mass pushing up into the pointed apex of the gastrula, and the same is true of *Aplysia* in which there are but two large blastomeres, though according to Blochmann's nomenclature such does not appear to be the case. In later stages the positions of the large cells of the fourth quartet of *Umbrella* and *Fiona* are identical. The intestine of *Umbrella* is said to be formed by C″ and D″ (5c and 5d), which, as Heymons did not take into consideration an entoblastic contribution from 4d, correspond fairly well to the conditions found in *Fiona*, where these cells lie just at the place of origin of the intestine and may well take part in its future development. The cell-lineage of the archenteron of *Crepidula* is given as follows: "The four macromeres form the roof of the archenteric cavity. The cells of the fifth quartet form its lateral boundaries, arching the cavity on all sides save the posterior. Here the archenteric cavity runs backward between the cells 5C and 5D (5c and 5d) nearly to the posterior boundary of the egg. The cells of the fourth quartet come together on the ventral side of the archenteron, forming its floor anteriorly and ultimately giving rise to some of the many small cells which form that part of the mesenteron, adjoining the stomodæum." The intestine arises from the posterior lower right region of the enteron as a tube-like evagination, formed from the enteroblasts derived from 4d and neighboring small endodermal cells and ending blindly against the ectoderm. Later it elongates and the end is carried somewhat upward along the right side by trosion of the larva. It contains a lumen from the first. As the stomach begins to enlarge it is seen to be bounded by large cells dorsally and anteriorly in its lower

regions. As development proceeds it is elongated, its posterior end being ventrally directed and turned toward the right. The development of the liver of *Crepidula* comes later, being retarded by the great amount of yolk.

The next change in the development of the enteron of *Fiona* may be observed in fig. 105, which represents a veliger in which the alimentary canal is beginning to become differentiated into several parts. Anteriorly is seen the stomodæum, which has as yet not broken through but touches the wall of the enteron. Above and to the left of this point of contact is a decided lobing of the wall of the enteric cavity, formed of the large yolk-ladened cells which at an earlier period lay in the anterior region of the archenteron. This is the rudiment of the liver, and as development proceeds the invagination becomes larger and more constricted at its base, forming a rounded lobe upon the left dorsal wall of the enteric canal. Behind the rudiment of the liver the enteron has widened into a capacious sac which is larger at its upper anterior end, the walls of the whole being formed of rather small cells which are yet rich in yolk. This is the stomach, and it ends blindly against the intestinal mass behind and to the right. The intestine is yet a solid strand of cells connecting the posterior end of the stomach with the ectoderm. With the growth of the veliger this strand has become more slender, elongated and turned forward, its distal end lying well up on the side of the body behind the constriction which forms the foot. The huge excretory cell lies just dorsal to this point (figs. 106, 107). In figs. 90, 91, 92 and 93, which represent coronal sections of a veliger somewhat older than figs. 105 and 106, and slightly more mature than that of fig. 107, it will be seen that the intestine is still a solid strand of cells, and that the œsophagus is as yet not in open connection with the rest of the alimentary canal. An examination of a considerably older larva (figs. 109, 110) shows a very small lumen, just beginning to form in the center of the intestinal strand, but as yet no communication between œsophagus and enteric cavity.

Stomodæum and Mouth.

As the blastopore narrows (fig. 79) it becomes entirely surrounded, except at the anterior end, by third quartet cells. At the anterior point second quartet cells from $2b^{22}$ and $2b^{212}$ lie along the edge also. Figures of a later stage (as 97, 98) show the blastopore as a mere rounded opening, its edges and walls below thickly set with darkly nucleated cells, and when complete closure occurs a plug of these cells

may be observed upon lateral optical section dipping down from the region of closure to the enteron beneath. These cells have come largely from the third quartet of all four quadrants, and represent the smaller cells of this quartet which lay nearest the open blastopore. This condition exists but for a short time, for soon a broad pit may be observed in this region occupying exactly the place where the blastopore closed. As it forms the cells which have been invaginated to form the blastopore-plug open out again so that a blind pit results, the lower surface of which is formed by those cells which were first pushed inward as the blastopore was closing, and correspond to the second and third quartet elements which are shown in fig. 79 surrounding the blastopore. The stomodæal invagination continues to increase in depth by growth and division of the cells which already form it and by further invagination of surrounding cells, so that, as the form of the veliger begins to appear (figs. 103, 104, 105, 106), second and third quartet cells from all the quadrants lying in the region probably become involved. At first the stomodæum is broad and shallow, but as it increases in depth it narrows and becomes more dorsally directed at its inner end. In section, fig. 90, and in drawings of the oldest veliger shown (figs. 109, 110), the stomodæal invagination has as yet not formed an open connection with the enteron, but shortly afterward this occurs, at which time the stomodæum is much elongated. Union is established with the stomach pouch just below the opening of the large liver lobe.

Fiona agrees with a large number of Mollusks in which the blastopore closes and the stomodæum forms at the same point. Among them may be named *Nassa* (Bobretzky), *Neritina* and *Aplysia* (Blochmann), *Elysia* (Vogt), various Æolididæ (Trinchese), *Doris* (Langerhans), *Crepidula* (Conklin), *Planorbis* (Holmes) and *Trochus* (Robert). In *Patella* (Patten), *Fusus* (Bobretzky), Pteropods and Heteropods (Fol) and *Limnæa* (Lankester) the blastopore is said to remain open and pass over directly into the mouth.

Shell-gland and Foot.

If one examines the segmenting egg somewhat later than such a stage as shown in fig. 73, it will be observed that the posterior has considerably outstripped the anterior region in extent and that, together with numerous divisions, the cells have also enlarged considerably in size. The area which lies along the median line, and so is derived from the second quartet, shows most plainly this rapid increase in extent, and it is here particularly that the cells themselves become greatly

enlarged and prominent. This is the region of posterior growth, and from this area arise both the shell-gland and the foot.

Taking up first the history of the former of these two organs, it will be found that in a stage represented by figs. 95 and 98 the whole area between the blastopore and the end of the posterior arm of the cross shows karyokinetic activity, but particularly in the region marked Sh.G. the cells have increased considerably in size. As growth continues these cells upon the upper and posterior surface of the gastrula protrude above the level of the ectoderm, the area which they cover having the appearance of a rough cobble-stone pavement; but somewhat later they settle down and form a smooth surface. The center of this area, which now lies just opposite the region of the stomodæum, begins to invaginate, pushing the enteron before it and reducing its cavity, so that there results a deep pit which, growing in size below, constricts above, and around which are several rows of large granular cells (fig. 102). Such a condition lasts but a short time, for soon the invaginated area opens outward, the whole forming a large thick-walled cap upon the posterior end of the veliger, constricted around its edge and merging abruptly with the thin-walled ectoderm anterior to it (fig. 104). As growth proceeds the shell-gland spreads and becomes much thinner, while the larval shell appears as a secretion of the large cells which compose it. As the shell continues to extend over the veliger its outer edge is marked by several rows of large cells, which by their secretive activity lay down the substance which forms the shell (figs. 105, 106, 107). Almost from its origin as a distinct structure the shell-gland is slightly displaced to the left side of the body, and as it increases in extent this lack of bilateral symmetry becomes more marked (fig. 107).

The ventral prominence which develops into the foot arises somewhat later than the shell-gland, and the cells which go into it come from the second quartet of D quadrant and the third quartet of C and D quadrants. The large ectodermal excretory cell, which in the larva lies just behind the foot, serves as a guide to show that much of the foot, like this cell, arises from C quadrant of the third quartet; and though no such landmark is present on the other side, the early history of the two quadrants are so similar that we may reasonably suppose a like origin from the third quartet for the left side of the foot. Lillie has derived the foot of *Unio* from cells of the second quartet, and Conklin appears to have done the same for *Crepidula*. Holmes states for *Planorbis* that as the cells immediately behind the blastopore are of third quartet origin, probably the "median portion of the anterior end

of the foot is derived from some of these cells". Robert describes a similar condition for *Trochus*. In *Fiona* not only the median portion but also much of the lateral area certainly comes from the third quartet. The foot here does not arise as a paired swelling as in *Patella* (Patten), *Fulgar* (McMurrich) and *Trochus* (Robert), but shows from the first a median protuberance which increases in size and later becomes broadened and flattened (figs. 103, 108, 110). Its upper surface is covered with numerous cells, but they are not arranged to form a conspicuous cell-plate as in *Crepidula*. Large cells mark its lower surface and they soon begin to secrete the operculum.

Larval Musculature.

It is particularly unfortunate that for a study of the muscles of the velum no living material has been available, as without this many points of interest must of necessity be lost. When the veliger breaks from its capsule it presents an appearance shown in figs. 109, 110, though it should be remembered that in fixed material, from which the drawings were made, the muscles must be much contracted. The whole posterior region is swollen into a huge transparent vesicle, at the anterior end of which lies the contorted alimentary canal. In dotted outline is represented the probable position of the cuticular-like shell before shrinkage. In a larva of such age one of the most characteristic features is a large dorsal retractor muscle, which has its posterior point of attachment well to the left of the dorsal side of the posterior vesicle. It runs forward and branches just before reaching the liver lobe, its two anterior ends becoming attached to the alimentary canal and the body wall in the region of the œsophagus. In structure it is composed of large spindle-shaped interlacing cells, which are flattened dorso-ventrally, giving the muscle a band-like form. In function this muscle doubtless acts as a retractor for the anterior and particularly the upper portion of the cephalic region. A dorsal view of the same veliger shows two lateral muscles, the right and left retractors of the foot, which arise about midway back on the sides of the posterior vesicle and extend forward through the lower part of the neck region, to end in branching fibers in the foot. That of the right side is larger than the left, and in earlier stages (figs. 105, 106) is much thicker than later and relatively larger. In figs. 105 and 106 is shown a small muscle (Vl.R.) extending from the dorsal neck region to the velar folds where it branches greatly. Other similar retractor muscles of the velar lobes extend from the walls of the alimentary canal and the body wall

outward into the velar area branching extensively. Fine interlacing fibers are also found in the foot in older stages.

Returning to the period marked by fig. 105, the dorsal retractor muscle is seen to be a short thick strand of cells extending from the shell region to the enteron near the position of the liver. It is here already branched and runs along the sides of the alimentary canal. The right retractor of the foot is, as shown, a very heavy cell strand which unites the foot with the lower dorso-lateral portion of the shell. A view from the left side would show a muscle occupying a similar position, but in this case much thinner (fig. 107 shows their relative sizes at a slightly later stage). Even at this early period the dorsal retractor is posteriorly attached to the left of the median line.

Bearing in mind the distinction of Lillie and others between primary mesoblast (ento-mesoblast) and secondary mesoblast (ecto-mesoblast or larval mesoblast), the attempt has been made to distinguish between these two sources of muscular tissue in the developing larva of *Fiona*, with, however, but partial success. The velar retractors, which lie in the region of the head vesicle, are formed from secondary mesoblast. Those cells which we have seen cut off from the third quartet in the two anterior quadrants lie in the antero-lateral region of the gastrula, and may for some time be distinguished from the primary mesoblast cells. When at an early period spindle-shaped muscle fibers appear in this region, their origin from these cells can scarcely be doubted. The component elements of the dorsal retractor are hard to distinguish. When this muscle first appears at a stage about midway between figs. 104 and 105, several large cells lie wedged in between the rounded wall of the enteron and the ectodermal area in the upper region of the shell-gland. The evidence is strong that these cells at least are from the primary mesoblasts. At this time, however, other cells extend along the enteron, connecting the compact posterior group with the loosely lying spindle-shaped elements of the velar retractors. They doubtless help form the more anterior portion of the dorsal retractor and, lying as they do so close to where secondary mesoblast was formed, may be derivatives of it. The two retractors of the foot and the interlacing fibers of that organ itself are doubtless composed of cells which have come from 4d. From the above account it is seen that a true "larval mesoblast" is found in *Fiona*, since much at least of the musculature of the velum, a purely larval organ, is derived from this secondary mesoblast.

No organ in any way comparable to a larval heart is to be found in the oldest veligers which I have studied.

Change of Axis and Form of the Developing Organism.

The egg at the time of laying is spherical. With the division into four cells the primary egg axis, running between the centers of the animal and vegetative poles, becomes shorter than the diameter of the equatorial plane. As segmentation proceeds this relation persists (fig. 14), and with continued division the formation of a large cleavage cavity becomes more pronounced. Until the cleaving egg reaches a stage of over sixty cells its surface, when viewed from either pole, appears almost perfectly rounded, but shortly after this its antero-posterior axis becomes shorter than the lateral (figs. 45, 56, 74), this relation holding until increased growth in the posterior and anterior quadrants causes elongation in that direction. Until about a stage shown in fig. 74 the primary egg axis, running from the center of the animal to the center of the vegetative pole, follows a straight line. Immediately after this, accentuated growth of the posterior region initiates a bending of this axis, which finally results in its complete folding upon itself, or a rotation through 180 degrees. A sharply pointed anterior projection arises (fig. 78), while at the same time the posterior dorsal region is rapidly increasing in extent and changing the embryonic axis. As the gastrula elongates the apical pole is moved forward, and by the time the first velar row becomes distinct the original polar axis has become so bent upon itself as to form an angle of nearly 90 degrees (figs. 95, 98). With the continued multiplication of cells in the head region that portion of the larva changes from its originally pointed shape into a rounded though not prominent head vesicle, while at the same time the opposite end is rounded by continued growth of second and third quartet elements (figs. 100, 101). The original polar axis will be seen in these figures to have moved through about 135 degrees. In the next stage, represented by figs. 102 and 104, the head vesicle has reached its largest relative size when taken in connection with the veliger as a whole. Comparing these figures with those which have gone before, a marked increase will be seen in the antero-posterior depth, and if this be considered in connection with the great change of axis the enormous growth of the posterior region will be evident. It is generally conceded that the head vesicle of molluscan and annelidan larvæ is of functional importance in serving as a float. In *Fiona* the head vesicle is never large and prominent and a substitute may reasonably be expected. With the differentiation of the velar lobes and foot the shell-gland may in figs. 105, 106 and 107

be seen to be rapidly spreading over the posterior region. As this is being accomplished it also grows greatly in size, producing the enormous posterior vesicle which in figs. 109 and 110 extends far behind the internal organs of the body. The importance of such an organ must be considerable and, taken in connection with the early decrease in size of the head vesicle, strongly suggests that its functional value is similar in kind to that usually ascribed to the anterior or head vesicle of other larvæ.

In all older veligers figured the original polar axis has become completely bent upon itself, a rotation of 180 degrees having occurred. With regard to the median plane of the future embryo, the first cleavage plane is obliquely transverse to this plane. When the mesoderm is formed it is thrown over toward this median plane, and from the first is approximately bilateral in position (figs. 24, 31, 34). The elements of both entoblast and ectoblast, which in late stages of cleavages lie on the median plane, appear to be derived from cells of the early cleavages which occupied similar positions. Little rotation, if any, is apparent other than a certain amount of irregularity found in all portions of eggs with equal or nearly equal cleavage.

Conklin describes for *Crepidula* an entire rotation of the ectoblastic cap at the time when the anterior and lateral cells of the fourth quartet arise. Heymons shows a similar rotation in *Umbrella*. Such a change of axis in the germ layers does not occur in *Fiona*, nor is there necessity for it. The large macromeres of *Crepidula* and *Umbrella* are here represented by small cells, which do not modify the positions of the germ layers at the time of their origin nor necessitate supplementary rearrangement.

Abstract.

Maturation begins at the time of laying. Two polar bodies are given off, the first of which may or may not divide. The unsegmented egg of *Fiona* is rich in yolk, the spherules being comparatively small. In shape the egg is round, but slightly flattened in the direction of its polar axis. One to three eggs are found in a roomy egg capsule.

The early cleavage is strictly spiral after the dextral sequence. The first quartet of micromeres are much smaller than the macromeres, but with succeeding divisions the cleavage becomes equal in character. After the four macromeres are formed they give rise to successive quartets of micromeres. The first three quartets contain all the ecto-

blast. The mesoblast arises in part from the fourth quartet cell of D quadrant. The remaining fourth quartet cells and all the macromeres are entoblastic, as is also the case with a small portion of 4d.

The first quartet of ectomeres give rise to the trochoblasts and ectoblastic cross. To the latter structure are added as "tips" the upper cells of the second quartet in all quadrants. The cross is radially spiral in symmetry, and does not increase in breadth by transverse splitting of its arms until a comparatively late period. Cells from the first quartet form the head vesicle, cerebral ganglia and eyes, and a portion of the first velar row.

The second quartet has a similar cleavage history in all four quadrants until a stage of about 150 cells. In later development the elements of this quartet in D (posterior) quadrant show great increase in size and divisional activity, initiating the posterior point of growth, with resulting bending of the embryonic axis. Cells from this area form the shell-gland and median portion of the foot. A large number of second quartet cells from the anterior and lateral groups aid in the formation of the velum. The more ventral elements of B quadrant help to close the blastopore.

In the third quartet bilateral cleavages first appear in the posterior quadrants (cells $3c^1$ and $3d^1$). Secondary mesoblasts arise from the anterior quadrant groups of this quartet (cells $3a^{2111}$, $3a^{2211}$ and $3b^{2111}$, $3b^{2211}$). The large anal excretory cell ($3c^{1111}$) and its associated cells are derived from C quadrant of this quartet. Third quartet cells surround the blastopore as it closes, with the exception of a small anterior portion; much of the stomodæum and the lateral portions of the foot come from third quartet elements.

The mesoblast of *Fiona* is derived from two sources, ento-mesoblast from 4d and ecto-mesoblast from the third quartet in A and B quadrants. The greater amount comes from 4d and forms teloblastic bands in the posterior region of the gastrula. The secondary mesoblast (ecto-mesoblast) is largely "larval" in fate, since much of it goes to form the muscles of the velum. From the history of 4d it appears that this cell contains both mesoblastic and entoblastic derivatives, the latter taking part in the formation of the intestine.

As is the case with many Opisthobranchs, the gastrula is sharply pointed anteriorly, the apical point at first lying at the end of the anterior arm of the cross.

The blastopore at the time of closure is surrounded by third quartet cells, except at its anterior edge, where second quartet cells are

present. The stomodæum later forms at the point where the blastopore closed.

The shell-gland at first forms a deep invagination, which later opens out and covers the posterior end of the veliger with a cap of large cells which soon begin to secrete the shell. From the first the shell is slightly shifted toward the left, and this asymmetry becomes more marked with continued growth. With the enlargement of the shell a conspicuous posterior vesicle results.

The foot arises as an unpaired swelling below the stomodæum. Its under surface later secretes an operculum.

The first velar row is formed from the anterior trochoblasts (A and B quadrants), the tips of the anterior arm of the cross, and possibly from other cells of the first quartet in this region. The second velar row is derived from underlying cells of the second quartet. A postoral velar area is but slightly marked. In later development the velum becomes bilobed and broadly expanded.

A prominent head vesicle is not present in the older veligers, and with this may be correlated the development of a large posterior vesicle. No apical sense-organ has been found, nor are distinctly marked apical plates present. The cerebral ganglia appear in the angles between the anterior and lateral arms of the cross. Otocysts are formed by invaginations of the ectoderm upon the sides of the foot, and pedal ganglia appear closely associated with them. The eyes are late in appearing and are intimately connected with the rudiments of the cerebral ganglia.

The anal kidney of the larva is derived from the ectoderm, coming from $3c^{1111}$ and associated cells. With the torsion of the larva this group is shifted farther to the right, and eventually lies well up on the right side of the veliger above the anal opening. Primitive excretory cells are also found lying in the body cavity laterally behind the velum.

The enteron is formed by invagination of the entomeres, which at first form an elongated sac; with the evagination of the shell-gland this becomes rounded. The liver is derived from large yolk-ladened cells lying at the anterior end of the enteron, and later the rudiment of this organ becomes turned toward the left side. Torsion of the enteron results from lengthening of the left side and is caused by increased growth of that region. The intestine is at first a solid thick cell-strand and is composed largely of entoblasts from 4d; it later elongates and acquires a lumen.

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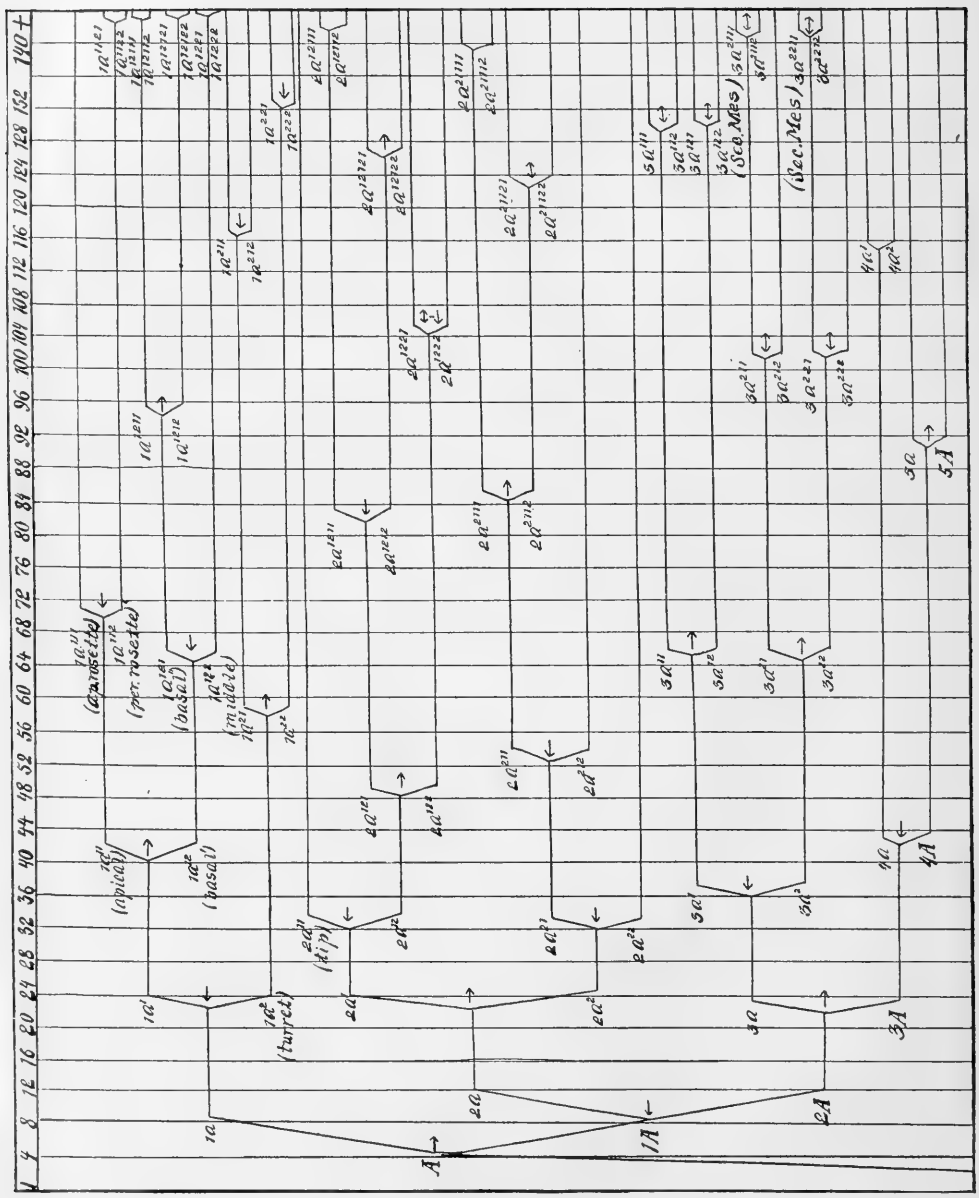
Table of Cell-Lineage.

A. QUADRANT.



Arrows pointing to right, dexiotropic direction of cleavage; to left, læotropic; double-headed arrows, horizontal; double-headed bent arrows in history of 4d, bilateral cleavages with relation to cells of opposite side.

Table of Cell-Lineage.

B. QUADRANT.

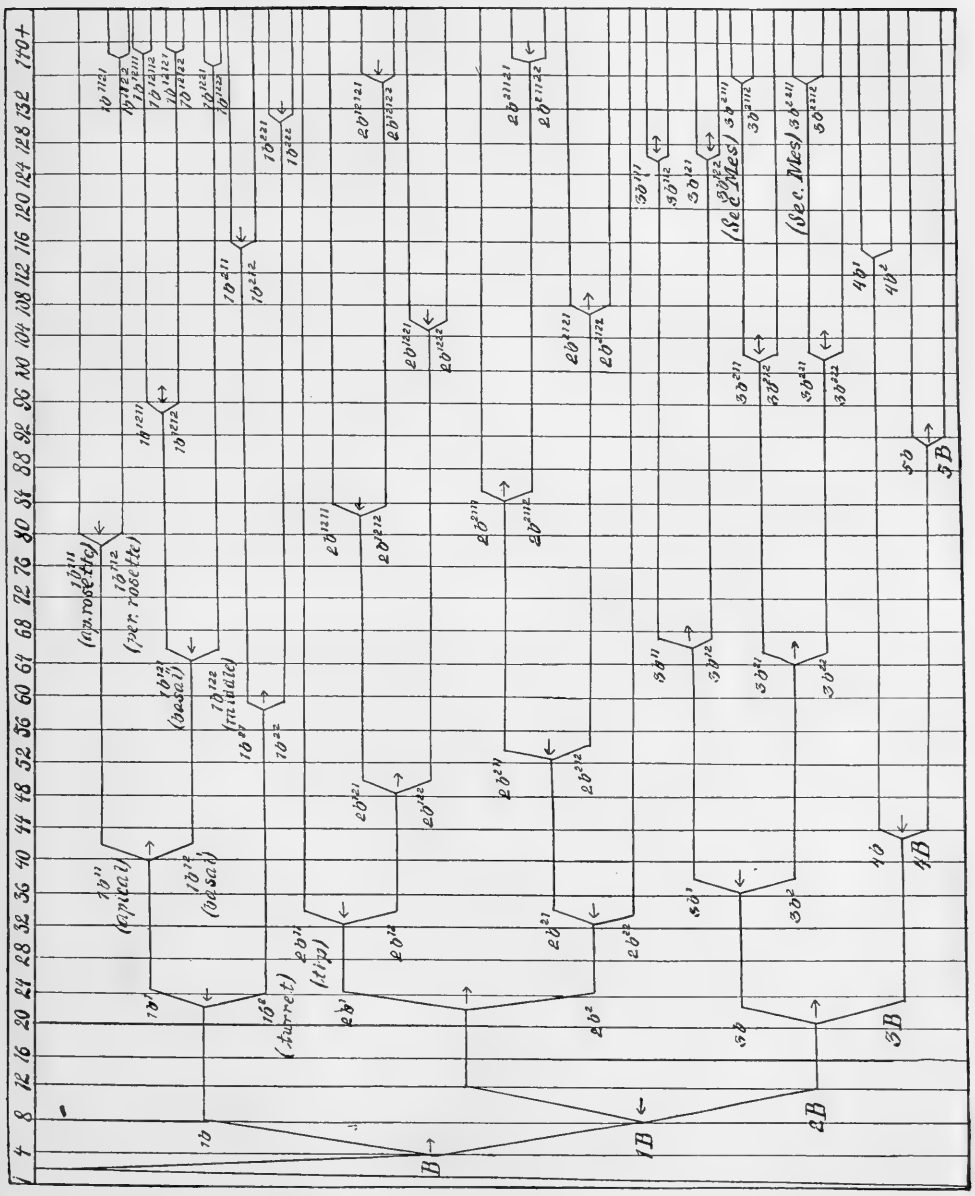


TABLE OF CELL-LINEAGE.

C. QUADRANT.

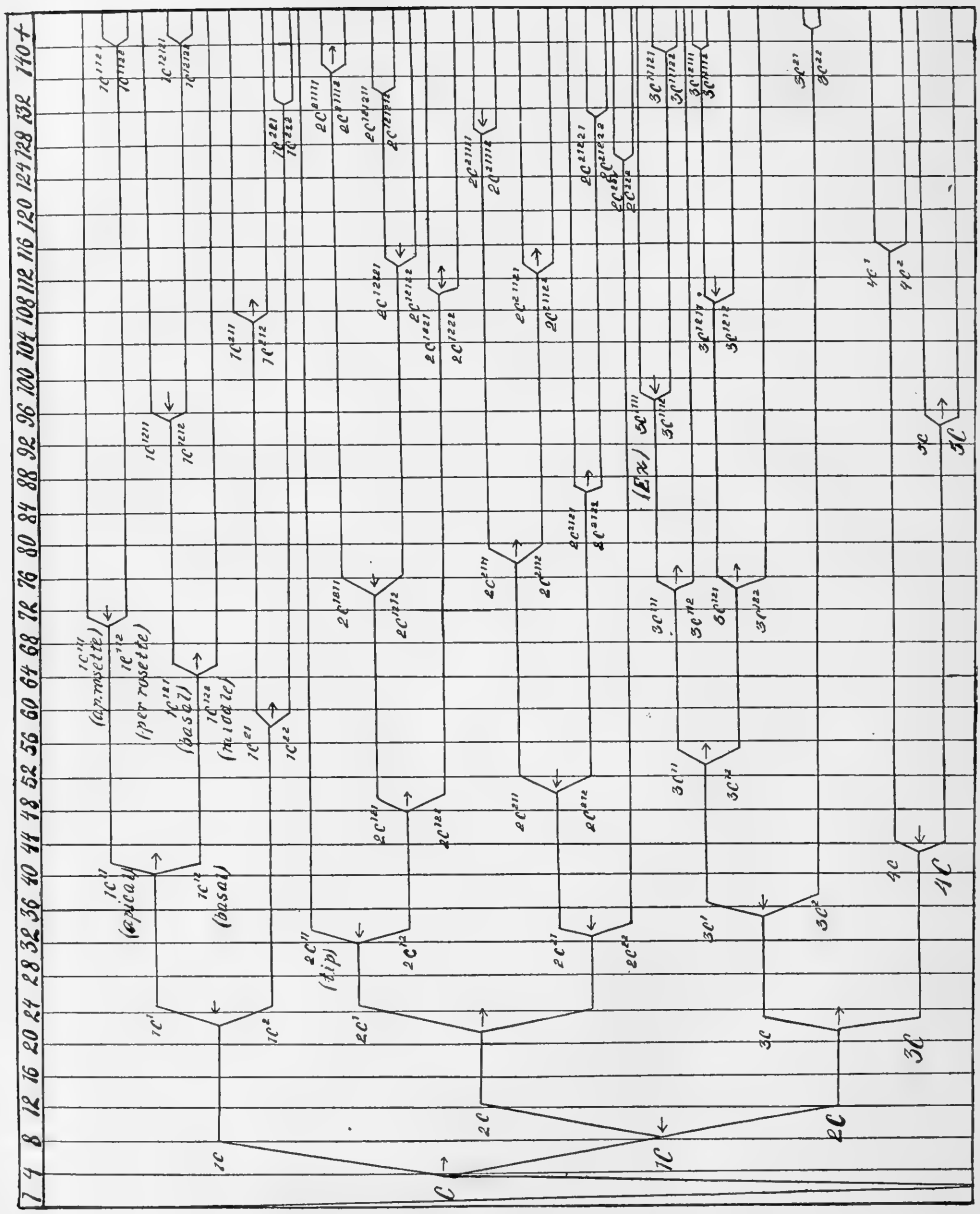
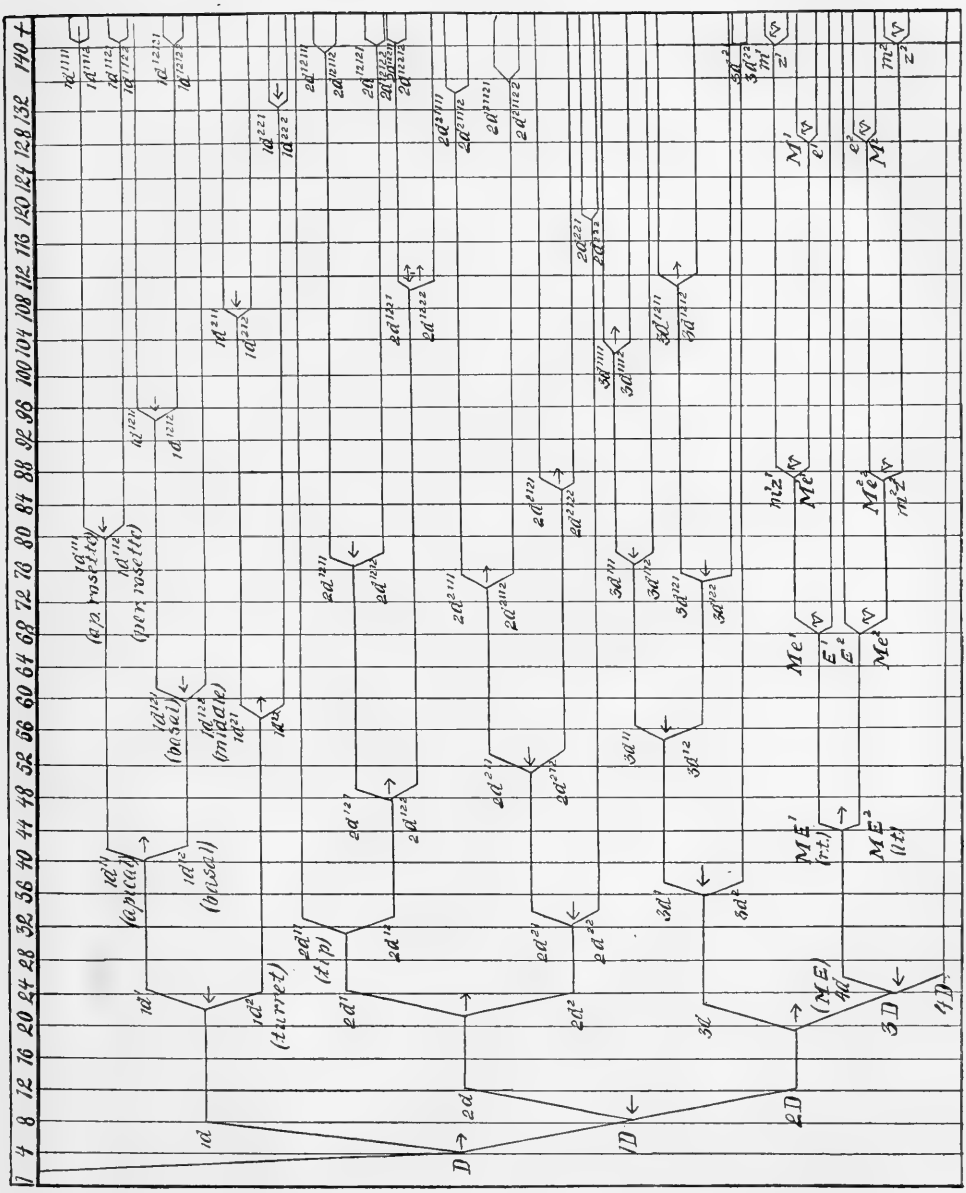


Table of Cell-Lineage.

D. QUADRANT.



Reference Letters.

Ap.....Apical point.
An.C.....Anal cell.
Bl.....Blastopore.
C.G.....Cerebral ganglion.
Dr.R.....Dorsal retractor muscle.
Ebl.....Enteroblasts.
E.C.....Large enteric cell.
En.....Enteron.
Ex.....Large anal excretory cell.
Ft.....Foot.
Int .....Intestine.
L.....Liver.
Lt.R.Ft.....Left retractor muscle of foot.
Mo.....Mouth.
M.F.....Muscles of foot.
Nph.L.....Left nephrocyst.
Nph.R.....Right nephrocyst.
Oes.....Œsophagus.
Op.....Operculum.
Ot.....Otocyst.
P.B.....Polar Body.
P.C.....Pedal Commissure.
P.G.....Pedal ganglion.
Rt.R.Ft.....Right retractor muscle of foot.
Sec.M.....Secondary mesoderm.
Sh.E.....Edge of shell.
Sh.G.....Shell-gland.
St.....Stomodæum.
Stom.....Stomach.
Tel.....Teloblast.
V^1.....First row of velar cells.
V^2.....Second row of velar cells.
Vl.L.....Velar lobe.
Vl.R.....Retractor muscle of velum.

Note.—In the drawings the trochoblasts are represented with stippled nuclei; upper pole views show the ectoblastic cross in heavy outline. Plates I–XI, XIII, and Figs. 101–104 of Pl. XIV are reduced ⅓ from original drawings, the remaining figures ½. Figs. 7, 36, 39, 46 and 55 have been omitted from Plates.

Explanation of Plates XXI–XXXV.

Plate XXI, Fig. 1.—Section of egg of *Fiona marina*, showing first maturation spindle.
Fig. 2.—Section. First polar body being given off. Sperm nucleus with astral rays below.
Fig. 3.—Section. Rise of second polar body. Enlargement of sperm nucleus and astral rays.
Fig. 4.—Lateral view of entire egg. Approach of male and female pronuclei.
Fig. 5.—First cleavage; figure seen from side.
Fig. 6.—Completion of first cleavage, as seen from above. The two polar bodies lie between the nuclei.
Fig. 8.—Completion of second cleavage, seen from upper pole. A polar furrow is present at the vegetative but not at the animal pole.
Fig. 9.—Upper pole view, showing spindles which institute third cleavage.

Plate XXII, Fig. 10.—Dexiotropic turning of spindles of the first quartet, with constriction and rounding out of these cells. Lateral view.
Fig. 11.—Same egg as fig. 10, seen from above.
Fig. 12.—Lateral view of slightly older egg than Fig. 10, showing compact grouping of blastomeres after division.
Fig. 13.—Completion of fourth cleavage, læotropic in direction, by which the second quartet is separated from the macromeres.
Fig. 14.—Lateral view of same egg as fig. 13.
Fig. 15.—Læotropic division of first quartet, by which the "turret cells" (trochoblasts), $1a^2$, $1b^2$, $1c^2$, $1d^2$, arise. In following figures the turret cells and their derivatives are indicated by stippled nuclei.
Fig. 16.—Lateral view of same egg as fig. 15.
Fig. 17.—First cleavage of the cells of the second quartet (dexiotropic). The macromeres are about to give off the third quartet by dexiotropic cleavage.

PLATE XXIII, Fig. 18.—Slightly later stage (lateral view) than fig. 17. Division of the second quartet is about completed.

Fig. 19.—Animal pole view of egg, in which the divisions shown in figs. 17 and 18 are fully completed. 24 cells.

Fig. 20.—Vegetative pole view of egg slightly older than fig. 19, showing spindle which initiates the separation of 4d.

Fig. 21.—Transition stage between 25 and 33 cells (seen from animal pole). All eight cells of the second quartet are dividing læotropically, the upper four forming the "tip" cells of the cross ($2a^{11}$, $2b^{11}$, $2c^{11}$, $2d^{11}$).

Fig. 22.—Same egg as fig. 21, seen from vegetative pole. The læotropic division of 3D, forming 4D and 4d (ME), is completed.

Fig. 23.—Animal pole view of egg containing 41–44 cells. $1a^1$–$1d^1$ have divided in a dexiotropic direction the "apicals" ($1a^{11}$–$1d^{11}$) and the "basals" ($1a^{12}$–$1d^{12}$) of the" ectoblastic cross."

PLATE XXIV, Fig. 24.—Same egg as fig. 23, seen from vegetative pole. All the third quartet cells have divided læotropically. The macromeres, 3A, 3B, 3C, are dividing in a similar direction to complete the fourth quartet.

Fig. 25.—View of vegetative pole of egg slightly older than fig. 24. The formation of the fourth quartet is completed and the mesentomere 4d (ME) has divided into right (ME^1) and left (ME^1) halves.

Fig. 26.—Lateral view from B quadrant of an egg same stage as fig. 25.

Fig. 27.—Lateral view of an egg, D quadrant, same stage as fig. 25.

Fig. 28.—Animal pole view of an egg showing, (1) dexiotropic divisions of $2c^{12}$, $2a^{12}$, $2b^{12}$; (2) læotropic division of $2b^{21}$; læotropic to horizontal division of $2c^{21}$. The trochoblasts, $1c^2$, $1d^2$, are also beginning to divide.

Fig. 29.—Same egg as fig. 28, seen laterally from B quadrant.

Fig. 30.—Same egg as fig. 28, lateral view of C quadrant; $3c^1$ is cleaving in a dexiotropic direction.

Fig. 31.—Vegetative pole view of same egg as fig. 28, showing bilateral divisions of $3c^1$, $3d^1$.

PLATE XXV, Fig. 32.—Lateral view D quadrant, slightly older stage than fig. 28, showing bilateral divisions of $3c^1$, $3d^1$.

Fig. 33.—Upper pole view of same egg as fig. 32, showing cleavage in three of the "basal" cells of the cross. $1b^{12}$ is dividing in a læotropic direction; in $1c^{12}$ the spindle is dexiotropic to radial in position; in $1a^{12}$ læotropic to radial spindle. The turrets, $1a^2$ and $1b^2$, show dexiotropic cleavage. About 60 cells.

Fig. 34.—View of vegetative pole of somewhat older stage than fig. 31; $3a^1$, $3a^2$, $3b^1$ and $3b^2$ have all divided in a dexiotropic manner.

Fig. 35.—Same stage as fig. 34, lateral view of C and D quadrants.

Fig. 37.—Lateral view of A quadrant, showing dexiotropic division of $3a^2$.

Fig. 38.—Upper pole view, showing completion of cleavage forming "basals" ($1a^{121}$–$1d^{121}$) and "middle" ($1a^{122}$–$1d^{122}$) cells of cross.

Fig. 40.—Slightly older stage than preceding, showing completed cleavage of $3b^1$.

Fig. 41.—Same egg as fig. 40, A quadrant.

PLATE XXVI, Fig. 42.—View of vegetative pole of egg with about 68 blastomeres. ME^1 and ME^2 are dividing bilaterally.

Fig. 43.—Lateral view, A and D quadrants of egg with about 75 blastomeres, showing dexiotropic cleavage of $2a^{211}$ and læotropic divisions in $3d^{11}$, $3d^{12}$.

Fig. 44.—Same egg as fig. 43, seen from C quadrant. $3c^{11}$ and $3c^{12}$ are dividing dexiotropically.

Fig. 45.—View of vegetative surface of egg with about 80 cells. The mesentomeres have divided into two small cells, E^1 and E^2, and two large, Me^1 and Me^2.

Fig. 47.—Same egg as fig. 45, lateral view of D quadrant.

Fig. 48.—Same egg as fig. 45, lateral view of C. quadrant.
Fig. 49.—Lateral view of D quadrant in egg of about 86 cells. $2d^{121}$ is dividing læotropically; $2d^{211}$ and $2d^{212}$ have divided dexiotropically.
Fig. 50.—Lateral view of same egg as fig. 49, showing A quadrant.

Plate XXVII, Fig. 51.—D quadrant, a lateral view. Me^1 and Me^2 all dividing bilaterally.
Fig. 52.—Lateral view, B quadrant of same egg as fig. 49.
Fig. 53.—Upper pole view of egg of about 86 cells. The "apical" ($1a^{111}$–$1d^{111}$) and "peripheral" ($1a^{112}$–$1d^{112}$) rosettes have been formed by læotropic cleavages.
Fig. 54.—Same egg as fig. 51, seen from side (C quadrant).
Fig. 56.—Upper pole view of an egg of approximately 106 cells. The basal cells, $1a^{121}$, $1b^{121}$, $1c^{121}$, have divided; $1d^{121}$ is dividing with spindle transverse to posterior arm of cross. The two inner posterior trochoblasts ($1c^{21}$, $1d^{21}$) are dividing bilaterally.
Fig. 57.—Vegetative pole view of same egg as fig. 56. Completed division of Me^1, Me^2 into M^1e^1, M^2e^2 and m^1z^1, m^2z^2.
Fig. 58.—Same egg as fig. 56, showing A and D quadrants on lateral view.
Fig. 59.—Same egg as fig. 56, principally B quadrant.

Plate XXVIII, Fig. 60.—Same egg as fig. 56, lateral view of C quadrant.
Fig. 61.—Lateral view, D quadrant, same egg as fig. 56.
Fig. 62.—Upper pole view of egg slightly older than last series (over 115 cells). All the interior trochoblasts have divided, and the completed transverse division of the basal cell of the posterior arm of the cross is shown.
Fig. 63.—Same egg as fig. 62, showing A quadrant on lateral view.
Fig. 64.—Lateral view, same egg as fig. 62, B quadrant.
Fig. 65.—Lateral view, same egg as fig. 62, C quadrant.
Fig. 66.—Lateral view, same egg as fig. 62, D quadrant.
Fig. 67.—Egg of about 125 cells, lateral view, C quadrant.

Plate XXIX, Fig. 68.—Same egg as fig. 67, lateral view of A quadrant.
Fig. 69.—Same egg as fig. 67, lateral view of B quadrant.
Fig. 70.—Slightly later stage than fig. 67, lateral view of C quadrant.
Fig. 71.—Entomeres and mesomeres from egg of over 150 cells, seen from vegetative pole.
Fig. 72.—Entomeres and mesomeres of egg about stage of fig. 71.
Fig. 73.—Entomeres and mesomeres, seen from vegetative pole of egg slightly older than the two former stages.
Fig. 74.—Vegetative pole view of about same stage as fig. 73, showing the overgrowth of the "secondary" mesoblasts (ecto-mesoblasts, $3a^{2111}$, $3a^{2211}$, $3b^{2111}$, $3b^{2211}$) by other cells of the third quartet.
Fig. 75.—Upper pole view, about the same stage as fig. 74, showing transverse splitting of the arms of the cross and division of outer trochoblasts.

Plate XXX, Fig. 76.—Upper pole view of somewhat later stage than fig. 75, showing increase in breadth of cross area.
Fig. 77.—Lateral view of stage similar to fig. 75, showing large excretory cell ($3c^{1111}$) and neighboring cells.
Fig. 78.—Vegetative pole view of gastrula with closing blastopore, showing pointed anterior end and complete overgrowth of the ecto-mesoblast.
Fig. 79.—Somewhat older gastrula than preceding figure.
Fig. 80.—Optical section (parallel to ventral surface) of gastrula of about the stage shown in fig. 79.

Plate XXXI (*except figs. 81–2*), Figs. 81–84.—Optical sections, similar in direction to that of fig. 80, through successively older gastrulæ, showing torsion of the enteron through increase in area of the left side (right

of figures). Fig. 84 represents a section taken through a young veliger about the stage of that shown in fig. 104.

Fig. 85.—Actual section through a gastrula similar in age to fig. 80 and in same plane.

Fig. 86.—Actual section (sagittal) through a gastrula about the age shown in fig. 95.

Fig. 87.—Actual section (about 30° to the right of the sagittal plane) through a young veliger slightly older than as shown in fig. 104.

PLATE XXXII (*except fig. 94*), Figs. 88–89.—Actual sections (nearly horizontal) through a veliger about the stage shown in fig. 105, showing cerebral and pedal ganglia, pedal commissure and otocysts; also large excretory cell on right side of larva and large enteric cell on same side of enteron.

Figs. 90–93.—Four successive horizontal actual sections through a veliger slightly older than that shown in fig. 107.

Fig. 94.—Nearly horizontal actual section through veliger of same age as preceding series, showing nerve ring around œsophagus. On Pl. XXXI.

PLATE XXXIII, Fig. 95.—Gastrula, seen from right side, showing first indication of the first velar row (V^1).

Figs. 96–97.—Upper and lower sides respectively of gastrula of the same age as shown in fig. 95.

Figs. 98–99.—Lateral (right) and lower sides of a veliger slightly older than that shown in figs. 96–97.

Fig. 100.—Left side of gastrula somewhat older than that shown in the two preceding figures.

PLATE XXXIV, Figs. 101–102.—Anterior and right-lateral views of larva midway between gastral and veliger stages. The deep invagination of the shell-gland (Sh.G.) has formed and the stomodæal pit (St.) is well marked.

Figs. 103–104.—Anterior and right-lateral views of a young veliger. The shell-gland has opened outward, the foot (Ft.) is becoming evident and the velar lobes are just beginning to appear.

Fig. 105.—Veliger, seen from right side, somewhat older than the preceding one, showing further development of velar lobes and foot, developing shell, differentiation of enteron and larval musculature.

Fig. 106.—Slightly older veliger than fig. 105, seen from right side.

PLATE XXXV, Figs. 107–108.—Dorsal and anterior views of the same veliger somewhat older than fig. 106. The shell and the velar lobes show considerable advance in development.

Figs. 109–110.—Right-lateral and dorsal views of the same veliger just before hatching. The dotted lines represent the probable shape of the posterior vesicle before shrinkage.

THE FOSSIL LAND SHELLS OF BERMUDA.[1]

BY ADDISON GULICK.

Last summer (1903), through advantages offered by the new Biological Station in Bermuda, I was able to collect the shells on which this paper is based. In the study of the material I owe much to Dr. H. A. Pilsbry, of the Academy of Natural Sciences of Philadelphia.

It will be necessary in the discussion of the fossils to compare them with the species that are now native, in the looser sense, to the islands. In drawing the line between these and the snails supposed to have been brought by commerce, I shall follow Dr. Pilsbry's latest paper on the "Air-breathing Mollusks of the Bermudas."[2] I shall also rule out all the littoral species, including *Truncatella*, because the fossil beds were not situated where such shells could be expected.

The most unsatisfactory feature of work on Bermudian fossil land shells is the difficulty in determining the ages of the various deposits. The rock of Bermuda is exclusively solidified dunes of calcareous sand, and the soil is the rust-colored residue of the weathered rock. In weathering, the surface of the rock becomes completely broken up into pockets and crevices packed with the earth. It is estimated[3] that every inch of earth must represent eight or nine feet of rock eroded, and thus when it is possible to judge of the average depth of soil formed over a deposit, that depth can be made an index of the age of the deposit.

Probably the oldest good fossiliferous deposit that I examined is collecting locality No. 807 (see Map No. 3) of the Bermuda Biological Station, at a hard-stone quarry on the west side of Knapton Hill, about midway between Hotel Frascati and "Devil's Hole." At this point a layer of eight or ten inches of red earth containing shells was covered by an ancient dune. The dune has become hard limestone, and its top has been eroded until now the red earth in its pockets must represent a layer averaging not less than six inches in thickness. The series of *Pœcilozonites* that we took from this bed is very incomplete, and the fossils of all the genera are poorly preserved, but notwithstanding this we are able to recognize at least eleven species and sub-

[1] Contributions from the Bermuda Biological Station for Research, No. 2.
[2] *Trans. Conn. Acad.*, Vol. X.
[3] A. E. Verrill, *Trans. Conn. Acad.*, Vol. XI, p. 490.

species. These are enough to identify its fauna with that of another deposit, locality No. 806 (see Map No. 2), where the shells are abundant and well preserved, but with no external evidence by which to estimate their age. This locality is another hard-stone quarry, where the excavations have uncovered a number of crevices and a cavern of considerable size. The shells are in stalagmitic conglomerate at the mouth of the cavern, and in the crevices, and also in the earth that fills certain of the pockets. They may represent a considerable period of time, but there is no way to distinguish any difference in age.

Another deposit at the same locality as the one last mentioned is a horizontal band of slightly reddish rock about half-way up the face of the quarry, and from two to three inches thick. This is part of the rock out of which the cave and pockets were eroded, so that the shells here are very much older than the others at No. 806; but here, again, there is no basis for a comparison with the date of No. 807. The remains here are obscure casts of *Pœcilozonites circumfirmatus* and of what appear to be *Vertigo* and *Carychium*.

I collected from three other beds in this neighborhood what seem to represent the same formation as the pockets of No. 806.

The first of these, locality No. 814, is a newly opened quarry just south from Coney Island. A red-earth pocket here contained a fine series of *Pœcilozonites nelsoni*, very large, but wanting the most extreme examples of both the elevated and the depressed variations. There are also fossiliferous conglomerates in caverns at this quarry, but they are composed of gravel too fine to contain *Pœcilozonites nelsoni*.

The best fossil specimens of *Pœcilozonites reinianus* came from locality No. 815, near Harrington House. They are noticeably larger than the recent specimens. No. 816, near 815, but on the shore of Castle Harbor, has large numbers of *Pœcilozonites bermudensis zonatus* and *Pœcilozonites reinianus*, the former associated with *Pœcilozonites nelsoni* in a conglomerate.

Bifidaria rupicola, found in the red earth of No. 806, may perhaps be an importation subsequent to the formation of No. 807, and *Strobilops hubbardi*, found at the same place, possibly may not have been a permanent resident; but we can safely assume that all the other species from the above localities belong to the epoch of the red-earth streak at No. 807. The remaining three deposits from which I collected are clearly much more recent than No. 807. These are in sand pits, in the nearly pure sand of partially solidified dunes. None of them have any clear signs of red earth, either about them or overlying them.

The shells at these places are so perfectly preserved that even the term "semi-fossil" seems a misnomer for them. Probably the sand preserves them by saturating the water with lime before it reaches them.

One of these shell deposits, locality No. 818, on the land of Mr. Benjamin Trott, in Tucker's Town, is only from 8 to 36 inches below the surface. The *P. nelsoni* were mostly in the upper foot of the deposit, where the bank is thoroughly solidified by the rain; but a few inches lower the sand is still loose enough to be scraped out with a strong hoe.

The two localities last to be mentioned, Nos. 808 and 809, are essentially alike. They face the Devonshire marshes on the northwest side—808 near the north end and 809 close to the barracks. The sand in these dunes appears to have drifted from near the present line of the north shore—a consideration which may yet give a clue to their age.

The following are my records of fossil and semi-fossil shells in these localities:

Locality 807.

Pœcilozonites nelsoni.
" nelsoni callosus.
" circumfirmatus, } Intergraded.
" discrepans. }
Euconulus turbinatus.
Zonitoides minusculus.
" bristoli. One specimen.
Thysanophora hypolepta.
Succinea bermudensis.
Vertigo numellata.
" marki?
Carychium bermudense.

Casts in the Rock, Locality 806.

Pœcilozonites circumfirmatus.
Vertigo.
Carychium?

Cave and Pockets, Locality 806.

Pœcilozonites nelsoni. Both extremes in height of spire.
" bermudensis zonatus.
" reinianus.
" circumfirmatus.

Pœcilozonites cupula.
Euconulus turbinatus.
Thysanophora hypolepta.
Succinea bermudensis.
Strobilops hubbardi.
Bifidaria rupicola. One specimen.
Vertigo numellata.
" marki.
Carychium bermudense.

Locality 814.

Pœcilozonites nelsoni, } In one pocket.
" reinianus. }
" nelsoni. In crevices.
" bermudensis zonatus, } In stalagmitic conglomerate.
" reinianus, }
" circumfirmatus, }
Euconulus turbinatus. }

Locality 815.

Pœcilozonites bermudensis zonatus? Small fragments only.
" reinianus.

Locality 816.

Pœcilozonites nelsoni.
" bermudensis zonatus.
" reinianus. (None kept in the collection.)
Euconulus turbinatus.

Locality 818 (Sand Pit).

Pœcilozonites nelsoni callosus.
" reinianus.
" discrepans.
Euconulus turbinatus.
Zonitoides bristoli.
Succinea bermudensis.
Bifidaria servilis. One specimen.
Carychium bermudense.

Locality 808 (Sand Pit).

Pœcilozonites bermudensis zonatus.
" reinianus.

Pœcilozonites circumfirmatus.
Euconulus turbinatus.
Succinea bermudensis.
Bifidaria rupicola. One specimen.
Carychium bermudense.
(Polygyra microdonta? One immature specimen, which may have crawled into the sand in recent times. We shall give it no further notice.)

Locality 809 (Sand Pit).

Pœcilozonites bermudensis zonatus.
" reinianus.
" circumfirmatus. (None kept in collection.)
Succinea bermudensis. (None kept in collection.)
Carychium bermudense.
Pupoides marginatus. One specimen.

These lists include all the known fossils except *Pœcilozonites dalli.*

Outside of *Pœcilozonites,* the species that do not appear in deposit No. 807 are:

Strobilops hubbardi.
Bifidaria rupicola.
" servilis.
Pupoides marginatus.

The last two of these appear only in the sand pits, and are in all probability later importations. The first two, found at No. 806, may also have arrived after No. 807 was covered up, but the fossils at No. 807 are so poorly preserved that we cannot presume upon the absence of these species. Ignoring these doubts, we may combine and rearrange the lists from Nos. 807 and 806—the more ancient fossils—mentioning after each species the habitat of its nearest relatives in other countries, as follows:

Pœcilozonites nelsoni.
" nelsoni callosus.
" cupula.
" bermudensis zonatus.
" reinianus.
" circumfirmatus.
" discrepans.

EUCONULUS TURBINATUS.
ZONITOIDES BRISTOLI.
VERTIGO NUMELLATA. } Eastern North America.
" MARKI.
CARYCHIUM BERMUDENSE.

[4]ZONITOIDES MINUSCULUS. North America and West Indies.
[4]BIFIDARIA RUPICOLA. Florida, Cuba.
[4]STROBILOPS HUBBARDI. Florida, Jamaica.
THYSANOPHORA HYPOLEPTA. West Indies.
SUCCINEA BERMUDENSIS. West Indies.

Total, 17 forms, 14 of them probably peculiar to Bermuda. For comparison we have the following *recent* species, supposedly not imported by man:

PŒCILOZONITES BERMUDENSIS,
" REINIANUS,
" CIRCUMFIRMATUS,
[5]ZONITOIDES MINUSCULUS, } Remnant of the fossil fauna. Seven species.
THYSANOPHORA HYPOLEPTA,
SUCCINEA BERMUDENSIS,
[5]BIFIDARIA RUPICOLA.

[5]PUPOIDES MARGINATUS. North America, West Indies.
[5]THYSANOPHORA VORTEX,
[5]POLYGYRA MICRODONTA,
[5]BIFIDARIA SERVILIS, } West Indies. Five species.
[5]BIFIDARIA JAMAICENSIS,
HELICINA CONVEXA.

Total, 13 species, 6 of them probably peculiar to Bermuda.

Dr. Pilsbry's conclusion, from the anatomy of *Pœcilozonites*, that the oldest importations to Bermuda came from continental America, is thus confirmed by a large majority of the fossil forms. Bermuda, at the time of the No. 807 deposit, was characterized by not less than five genera of continental affinities, of which at least one had been resident long enough to have developed new generic characters and a respectable diversity of species. The abundance of the individuals, too, and the size and variability of some of the species, seem to show that the island was not inhospitable to continental genera at that epoch. There were not only the large extinct species *Pœcilozonites nelsoni* and *Pœcilozonites cupula*, but larger varieties also of *Pœcilozonites bermudensis* and

[4] Species not peculiar to Bermuda.
[5] Species not peculiar to Bermuda.

Pœcilozonites reinianus than are now living. The largest specimens even of *Pœcilozonites circumfirmatus* and *Succinea bermudensis* are among the fossils. These snails must have found more food than there is now on the uncultivated ground. There is also geologic evidence that they belonged to a more prosperous epoch than the present. Prof. Heilprin reports that in excavations for one of the docks, specimens of *Pœcilozonites nelsoni* were brought up from a peat deposit at a depth of forty feet below water. A rise of the land sufficient to put these shells ten feet above sea-level (see Map No. 1) would multiply the land area eight or ten times, changing it from a narrow ridge, hardly two miles wide at its widest, into an elliptical area, including, it is true, some large lagoons, but in all about ten miles across and more than twenty miles long. A large, protected interior valley would then receive the fertile soil that is now washed into the lagoon by every storm. It would not surprise me if the deposits at locality 807 should be shown to date from the period of this Greater Bermuda, but a person need hardly wait for this proof before supposing that the indigenous contemporaries of *Pœcilozonites nelsoni* were also characteristic of Greater Bermuda.

In spite of their evident prosperity, I do not think it could be proved that these snails lived under any densely shading vegetation. The humidity at Bermuda makes such a shade less necessary for snails than it is in many places. I have often seen *Succinea bermudensis* clinging to grass and to trunks of trees in such situations that I imagine an American summer day would have desiccated them. The tract about Prospect Hill (No. 809) must have been desolate, unshaded land when the hills were growing dunes, yet the sand here (localities 808 and 809) contains numerous well-developed specimens and quite a variety of species. These must either have lived where they are found, or else have been blown there from some place almost equally windswept.

The extinction of species that were able to prosper on those barren parts of the island seems to me a strange occurrence. If, as I believe is probable, the sand for these dunes came from near the present north shore, then the island must have had very nearly its present shape and size when these snails were alive. Thus when the Greater Bermuda sank, the change seems to have set new dunes in motion across this section of the Lesser Bermuda; and *Pœcilozonites zonatus*, *Carychium bermudense* and *Euconulus turbinatus* not merely survived the subsidence, but even formed a considerable population on the parts of the remaining island that were most damaged by the changing condi-

tions. How many other species still survived in the less altered sections it is impossible to say. It is hardly possible to prove that even the set of fossils from No. 806 belong to any earlier date. Indeed we might draw an analogy between *Bifidaria rupicola* at No. 806, which may be one of the later arrivals, and *Bifidaria servilis* at No. 818 and *Pupoides marginatus* at No. 809, either of which we can hardly hesitate to treat as recent arrivals. But however this may be, the sand-pit deposits are against the supposition that the *Carychium* and its hardier associates were exterminated merely by the increasing barrenness of the island. We should be in a better position to discuss the other causes if we knew whether these species survived till after the West Indian arrivals had begun to take possession of the land. The West Indies snails, especially *Polygyra microdonta*, of Bahama, are at present much the commonest of the "native" snails, and it may be that their special fitness for the more barren land of the new Bermuda made them deadly competitors to the old species. The newer formations at the west end of the islands, which I had not the time to visit, may perhaps be the ones in which to look for evidence on this question.

Notes and Descriptions.

Thysanophora vortex Pfr.

Living animals quite abundant under stones; but I looked in vain for fossil specimens. Greater Antilles, Bahamas, Southern Florida.

Thysanophora hypolepta 'Shuttl.' Pils.

I found more examples of this than of *Z. minusculus* among the fossils, but among the living snails *Z. minusculus* seems to be far more abundant. It is supposed to be indigenous.

Polygyra microdonta Desh.

Excluding importations from Europe, this species is the one now most in evidence. It is partial to the coarse native grass, but is to be found almost everywhere. I was surprised not to find any indubitable specimens of this in the sand pits. I hope other collectors will look for it. Bahamas.

Strobilops hubbardi Brown.

An adult and an immature specimen, from locality 806. The adult is somewhat larger than the usual size on the continent. Alt. 1.2, diam. 2.8 mm. Habitat, the Gulf States and Jamaica.

Vertigo numellata n. sp. Pl. XXXVI, fig. 6.

Shell rimate, minute, elliptical or bluntly pupiform, yellowish-corneous, faintly striate, of 5 rather convex whorls; the diameter through the body whorl not much greater than that through the whorl

preceding. A prominent, whitish, inflated ridge, appearing like a second peristome, occurs behind the peristome. Aperture proportionately more contracted than that of *V. ovata;* set with a parietal, an angular and a columellar lamella; and with two palatal and a basal fold. The palatal folds are prominent, the upper one slightly double-topped, the lower one more immersed and entering spirally. The parietal lamella is stout and blunt; the angular lamella smaller and thinner; the columellar lamella and the basal fold low and blunt. Peristome rather thin, expanded, and notched opposite the upper palatal fold, as in *V. ovata.*

Alt. 1.7, diam. .9 mm.

In one specimen there appears a slight suprapalatal denticle. A considerable number of smaller, more globose specimens seem to belong to this species. One of these from locality 806 measures 1.4 x .9 mm.

I have assumed that this species is more closely related to *V. ovata* than to any of the species reported from the West Indies.

Localities 806 and 807; the type from 806.

This is the common fossil *Vertigo.*

Vertigo marki n. sp. Pl. XXXVI, fig. 7.

Shell rimate, ovate, yellowish-corneous, faintly striatulate; whorls nearly 5, rather convex. Apex obtuse, but not rounded like that of *Vertigo numellata.* The inflated ridge inconspicuous, whitish, crowded close to the peristome. Aperture ovate, much longer than in *Vertigo numellata,* set with four denticles, of which the parietal lamella is the largest. The lower palatal fold denticular, smaller than that of *Vertigo numellata* and less immersed; the upper palatal fold minute; and the columellar lamella broad and low. The peristome is expanded, white, strongly thickened within, hardly notched at the upper palatal fold.

Alt. 1.9, diam. 1 mm.

Named in honor of Dr. E. L. Mark, of Harvard, Director of the Bermuda Biological Station for Research.

This species is somewhat suggestive of *V. tridentata,* but is a little slenderer, with a longer aperture, and a heavy white peristome.

Locality 806; doubtful specimens from 807.

Bifidaria rupicola Say.

One specimen each from localities 806 and 808, and several recent specimens. Dr. Pilsbry reminds us that the Bermudian form has a thicker lip than the others of this species. Cuba, Florida.

Bifidaria servilis Gld.

One specimen from locality 818, and a few recent. Cuba and other West Indian islands.

Bifidaria jamaicensis C. B. Ad.

The commonest of the recent Pupidæ, but I failed to find it fossil. Greater Antilles.

Pupoides marginatus Say.

I got one indubitable specimen from locality 809, but it went to pieces in my hands. I found only two or three recent ones. Mr. Owen Bryant, who was collecting at the same time, found a larger number. Eastern and Central North America, and some West Indian islands.

Carychium bermudense n. sp. Pl. XXXVI, figs. 11, 12.

Shell almost regularly tapering, corneous-white, imperforate, finely striate; whorls about 5, increasing regularly, those of the spire very convex, with deep sutures. Aperture quite oblique, obstructed by a small parietal and a very minute, deeply placed columellar lamella. Peristome broadly expanded and reflexed, thickened within by a white callus, with a slight groove on its front face, and developed inward to form a prominence slightly above the middle of the outer margin (near the position of the upper palatal fold in *Bifidaria*).

Alt. 1.8, diam. .9 mm.

This species is very dissimilar to the slender *Carychium jamaicense*. The shape of the aperture allies it more nearly to *Carychium exiguum* of North America, but its heavy peristome is quite its own.

It is one of the most abundant fossil species, occurring in the red earth of localities 806 and 807, and even in the sand that fills the larger shells in the sand pits.

Pœcilozonites nelsoni (Bld.).

Hyalina nelsoni Bld., Ann. Lyc. N. H. of N. Y., XI, 1875, p. 78.
P. nelsoni Pilsbry, Proc. Acad. Nat. Sci. Phila., 1888, p. 290.
P. nelsoni v. Mart., Sitzungsber. Ges. Nat. Freunde, Berlin, 1889, p. 201.

The typical form of this species is, I suppose, the large, moderately elevated form. This is represented among my specimens from locality 814, where the variation in dimensions is as follows:

Alt. 29	Diam. 39 mm.
28	37
27	41
27	40
26	35
25	39
23.5	36
23	41.5
23 (estimated)	35

The way these lay, piled together in a little pocket, compels the supposition that they lived at about the same time, and their varia-

tions in outline show what may occur in a single intergenerant colony. The specimens from locality 806 show even greater differences, of which the following are the extremes:

Alt. 34	Diam. 34 mm.
31	33
19	37
19.5	39

I should like to suggest the name *discoides*, merely as a convenient term by which to know the variation represented by the last two shells (Pl. XXXVI, fig. 4). I must say, however, that this suggestion would be unfortunate if it resulted in the division of the series obtained from locality 814. It seems to me, rather, that some physiological peculiarity has destroyed the diagnostic value of the elevation of the spire. The upper whorls differ less than the lower, and in the most elevated forms the suture of the later whorls is much below the keel of the preceding whorl, as if the slant of the spiral had been abnormally diverted downward.

Pœcilozonites nelsoni var. **callosus** n. var. Pl. XXXVI, fig. 5.

Shell smaller than the typical form, shiny, with heavy ribbed striæ, colored with a broad yellowish-brown peripheral band on a white ground. Whorls a trifle more than nine, increasing regularly and very gradually. The suture does not change its character nor become deflected from the peripheral line of the preceding whorl. The usual peripheral angle is almost obsolete. The base has a stronger angle about the umbilical perforation than is usual in the species. The peristome is greatly thickened on the inside from 1 mm. at the suture to fully 2 mm. near the columella. A prominent callosity covers the parietal wall of the aperture.

Alt. 24, diam. 33 mm.

The combination of small size and large number of whorls is characteristic. The ratio of height to diameter is more constant than in the typical form, and the tendency to produce the callosity is very marked.

Type from locality 818, others from 818 and 807.

The stability of the variety, occurring as it does in the oldest and the latest formations, is the most interesting thing about it. It is also my excuse for regarding such slight distinctions in a remarkably variable species.

I suppose the color patterns of *Pœcilozonites nelsoni* were essentially the same as those on the living *Pœcilozonites bermudensis*. For example, the type specimen of *callosus* probably had a dark brown band

on a background of a yellowish cuticular color. The depressed specimen which is figured has traces of a subperipheral band, a supraperipheral line, and radial flaming above this line. This flamed pattern appears in several of the flat specimens.

Pœcilozonites cupula n. sp. Pl. XXXVI, fig. 2.

Shell solid, dome-shaped, with somewhat flattened base, perforate, strongly striate; pale, shiny-corneous, with subsutural and subperipheral bands of darker color, and faint traces of two narrow bands on the periphery. Whorls $7\frac{2}{3}$, a little convex, increasing slowly; the last vaguely angulate at the periphery. The aperture is somewhat quadrangular on account of the straight, vertical columella and the peripheral angle. The peristome is simple, thin, with the columellar margin reflexed.

Alt. 13 Diam. 16 mm.

Locality No. 806.

Other specimens measure:

Alt. 13.5	Diam. 16.5 mm.
12.5	17
13	19
13	20
15	15.5

The last specimen has $8\frac{3}{4}$ whorls.

The type was selected as the best-preserved specimen, not as the most representative example. The majority of the specimens have a more rounded base and periphery, giving the peristome a more oval contour. The height of the shell and the absence of a keel distinguish it readily from *P. bermudensis zonatus,* and the very round dome and less angulate periphery separate it from immature specimens of *nelsoni.*

Pœcilozonites dalli n. sp. Pl. XXXVI, fig. 1.

Shell elevated, with rounded apex and convex base, perforate. Its surface is polished, with incremental lines less pronounced than those of *P. cupula;* milky-white, with a yellowish-brown band below the periphery and a line above the periphery. The first four whorls are translucent whitish. Whorls $7\frac{1}{6}$; all but the final whorl are flat as if keeled, that one has a blunt peripheral ridge, below which it is deeply rounded. The aperture is quite oblique, round-lunate. The peristome is simple, except at the columella, which it joins without an angle, but the columellar margin is reflexed, partly covering the perforation.

Alt. 8.5 Diam. 7.3 mm.

Another specimen has the height 10, diam. 7 mm., and is composed of 9 whorls. It shows more of the brown and less of the white color.

The extreme variability of *P. cupula* leaves it debatable whether this may not be a dwarf race of that species.

No specimens of this form were found last summer, and it is through the courtesy of Dr. William H. Dall of the National Museum, that I am able to describe and figure it. The specimens came to him without labels, so that we are left to conjecture their age. The slender specimen is so glossy and brightly colored that Dr. Dall doubts whether it can be a fossil, but it seems to me the simpler hypothesis to suppose that it was preserved in the sand in the same manner as the type of *P. nelsoni callosus*, which it so closely resembles in color and polish. The shell sand seems to be a complete protection from destructive agents. On this hypothesis it had originally about the color of *Pœcilozonites bermudensis*.

Pœcilozonites bermudensis Pfr.

Pilsbry, Proc. Acad. Nat. Sci. Phila., 1888, p. 289; 1889, p. 85.

The typical variety seems to be of recent origin. It is distinguished from the fossil by a less rounded upper surface, less flattened apex, larger umbilical perforation, and usually smaller number of whorls. My largest specimen I found on Rabbit Island, Harrington Sound, buried under drift sand at some time previous to the cultivation of the island. It measures alt. 13, diam. 24.5 mm. The largest and smallest living mature shells measure as follows:

Alt. 14.5	Diam. 20. mm.
14	22
10	16.5

An average fully adult specimen measures:

Alt. 11 Diam. 20 Umb. 1.7 mm.

and has a trifle more than 7 whorls.

Pœcilozonites bermudensis var. **zonatus** Verr. Pl. XXXVI, fig. 3.

This differs from the type of the species in possessing an almost uniformly curved upper contour line, an almost flat apex, and a more constricted umbilicus. The keel is distinct, as in the recent form. Whorls 7⅔. The aperture is surrounded by callous thickenings as in *P. nelsoni callosus*. Alt. 13.5, diam. 23, umb. 1 mm.

Specimens come from localities Nos. 806, 808, 814, 816 and 809.

The extremes from locality No. 808 are:

Alt. 16	Diam. 22.5 mm.	
15	25	
12.5	20.5	Umb. 1 mm. wide.

Thus the smallest adult is quite equal to the average recent shells. A few selected specimens of the fossil and recent shells can hardly be distinguished. Many of the fossils do not have the callosity.

Locality 816 has great quantities of these shells so firmly cemented together that most of them are worthless as specimens. They have the peculiar spheroidal upper surface, but the perforation is wider than in the series from locality 808—not so wide, however, as in the recent. Several specimens here occur below some fragments of *Pœcilozonites nelsoni* in stalagmite, apparently showing that they were there previous to the extinction of *nelsoni*.

Broken and immature specimens from locality 808 show that the umbilicus was not much narrower than that of the recent variety until the last whorl had commenced to grow. The peculiar contour is also less noticeable prior to the last whorl. Thus in their smaller number of whorls, their less rounded contour, and their larger umbilicus, the present snails seem like an undeveloped or degenerate race of the former species.

It is possible that this fossil variety is what Pfeiffer (*Monographia*, I, p. 80) mistook for *Helix ochroleuca* Fer.

Pœcilozonites reinianus Pfr.

Helix reiniana Pfeiffer, Malak. Bl., XI, 1863, p. 1.
P. reinianus Pilsbry, Proc. Acad. Nat. Sci. Phila., 1888, p. 290; 1889, p. 85.

I found this species in every deposit examined except No. 807. Further search would doubtless show it there also. At locality 815 many fine specimens were embedded in stalagmite. They show the typical color-pattern, with the dark marks changed as usual to reddish, and the lighter ground to ivory-yellow.

The largest specimen from No. 815 measured....	Alt. 7	Diam. 13	mm.
The largest from No. 808		12	
The largest from No. 806		11.5	
The largest from the pocket at No. 814		11	
The largest recent, lent by Mr. Bryant	6	11.3	
My largest recent	5	10.3	

From Town Hill (locality 819) come some good specimens of var. *goodei* Pils. Examples of these measure:

Alt. 4	Diam. 10	Umb. 4	mm.
3.5	9.3	3.4	
3.7	10	4	

The species is not so uniformly common as *Pœcilozonites circumfirmatus*, but is very abundant in some places, for example, near locality 806. It would be interesting to learn whether its place in the economy of nature is different from that of the following species.

Pœcilozonites circumfirmatus Redf.

Helix circumfirmata Redfield, Ann. Lyc. N. H. of N. Y., VI, p. 16.
Pœcilozonites circumfirmatus Pilsbry, Proc. Acad. Nat. Sci. Phila., 1888, p. 291.

The modern variety comes from both formations at locality 806, and from 814 and 808. Those from locality 808 are some of them more keeled than is now usual. A series of poor specimens from No. 807 seem to bridge the gap from these to var. *discrepans*.

This species has lost less in size than the others of its genus. My largest fossil, coming from locality 808, has alt. 7, diam. 12 mm. My largest recent shell has alt. 7, diam. 11.5 mm. I think the fossils average larger than the adults of the recent shells, but it is not easy to eliminate the immature of either.

Pœcilozonites circumfirmatus var. **discrepans** Pfr.

Helix discrepans Pfr., Malak. Bl., 1864, p. 1.

Localities 807, 818 and two specimens of doubtful identity from 806. Some from 818 are extremely flat and carinate, one of them having alt. 4.8, diam. 10.5 mm. If this were the only locality that yielded the variety it would undoubtedly rank as a distinct species.

I should like to raise the question whether *Pœcilozonites discrepans* is not one of the extinct varieties. I believe it has not been treated as such heretofore, but none were found last summer any more recent than those from this sand pit.

Euconulus turbinatus n. sp. Pl. XXXVI, figs. 8, 9, 10.

Shell acutely conic, with contour very slightly convex; minutely perforate, thin, glistening yellowish-corneous, closely striate, and sculptured with microscopic spirals. Apex rounded off abruptly. Whorls $7\frac{1}{2}$, not convex, narrow, the last strongly angulate at the periphery. Suture simple, hardly impressed. Base rather flat, not excavated. Aperture almost quadrangular, but with the angle at the columella indefinite. Columella slightly curved, the columellar margin narrowly reflexed. Alt. 3.4, diam. 2.8 mm. (from locality 807); diam. 3 mm. (from locality 808).

From localities Nos. 807, 806, 814, 816, 808, and 818.

The above description is a composite. The general form is described from the specimen from locality 807, but the sculpture is that of the best specimen from 806, which should, perhaps, be considered the type, and the base and aperture are taken from the specimen from 808. From 814 comes the longitudinal section of one 3.8 x 2.8 mm., with an unusually convex contour.

The genus *Euconulus* is of course, not wholly satisfactory for this species.

Zonitoides minusculus Binn.

Locality 807, and recent. Its abundance in the one deposit and absence in the others is a little surprising.

Zonitoides bristoli n. sp. Pl. XXXVI, fig. 13.

Shell resembling *Zonitoides minusculus* in general form, but much smaller, only moderately umbilicate, white, costulate, and densely sculptured with spiral lines; composed of 3 convex whorls. Apex somewhat elevated. Aperture lunate, the outer and basal margin more uniformly curved than in *Zonitoides minusculus*, and the preceding whorl cutting out a greater arc. Peristome simple, thin. Costulæ regularly spaced, coinciding with growth lines. The spaces between them crowded with fine striæ. A close, regular, spiral sculpturing crosses these lines and gives the costulæ a slightly tubercular appearance.

Alt. .7 Diam. 1.17 mm.

Named in honor of Dr. C. L. Bristol, of New York University, Associate Director of the Bermuda Biological Station for Research.

One specimen from each of localities 807 and 818; the type from the latter place.

Succinea bermudensis Pfr.

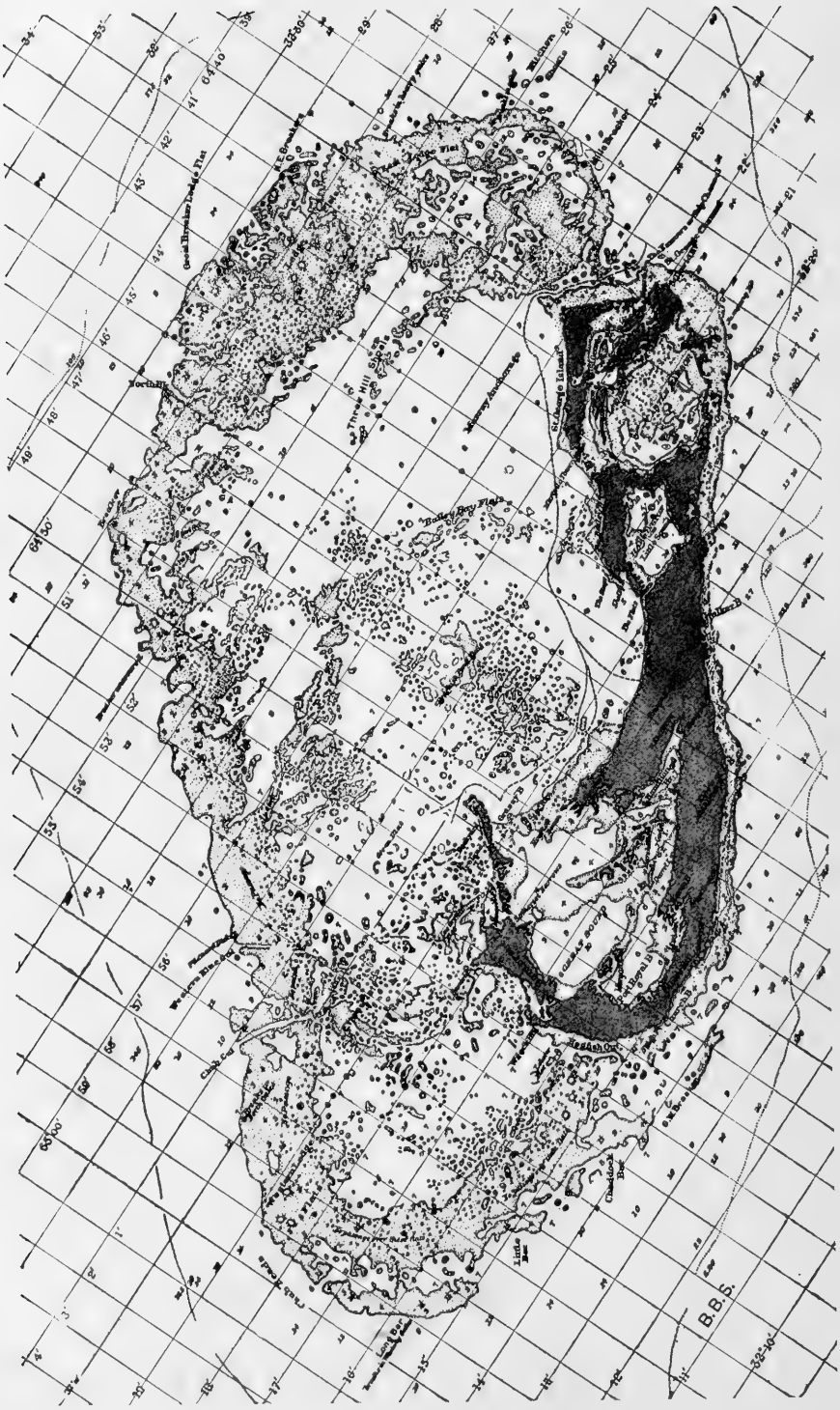
S. bermudensis Pfr., P. Z. S., 1857, p. 110; Monographia, IV, p. 817.
S. barbadensis Pilsbry, Trans. Conn. Acad., X, p. 502.

Localities 807, 806, 818, 808, 809 and recent. In the absence of alcoholic specimens of *S. barbadensis* I have given up that name and returned provisionally to the name *bermudensis*. Its presence as a fossil makes it not unlikely that it may be proved distinct from *S. barbadensis*. This is another species that was formerly larger than now. The largest fossil, from locality 808, measures alt. 13, diam. 7 mm. The largest out of 30 recent specimens lent by Mr. Bryant has alt. 12, diam. 6.3 mm.

Helicina convexa Pfr.

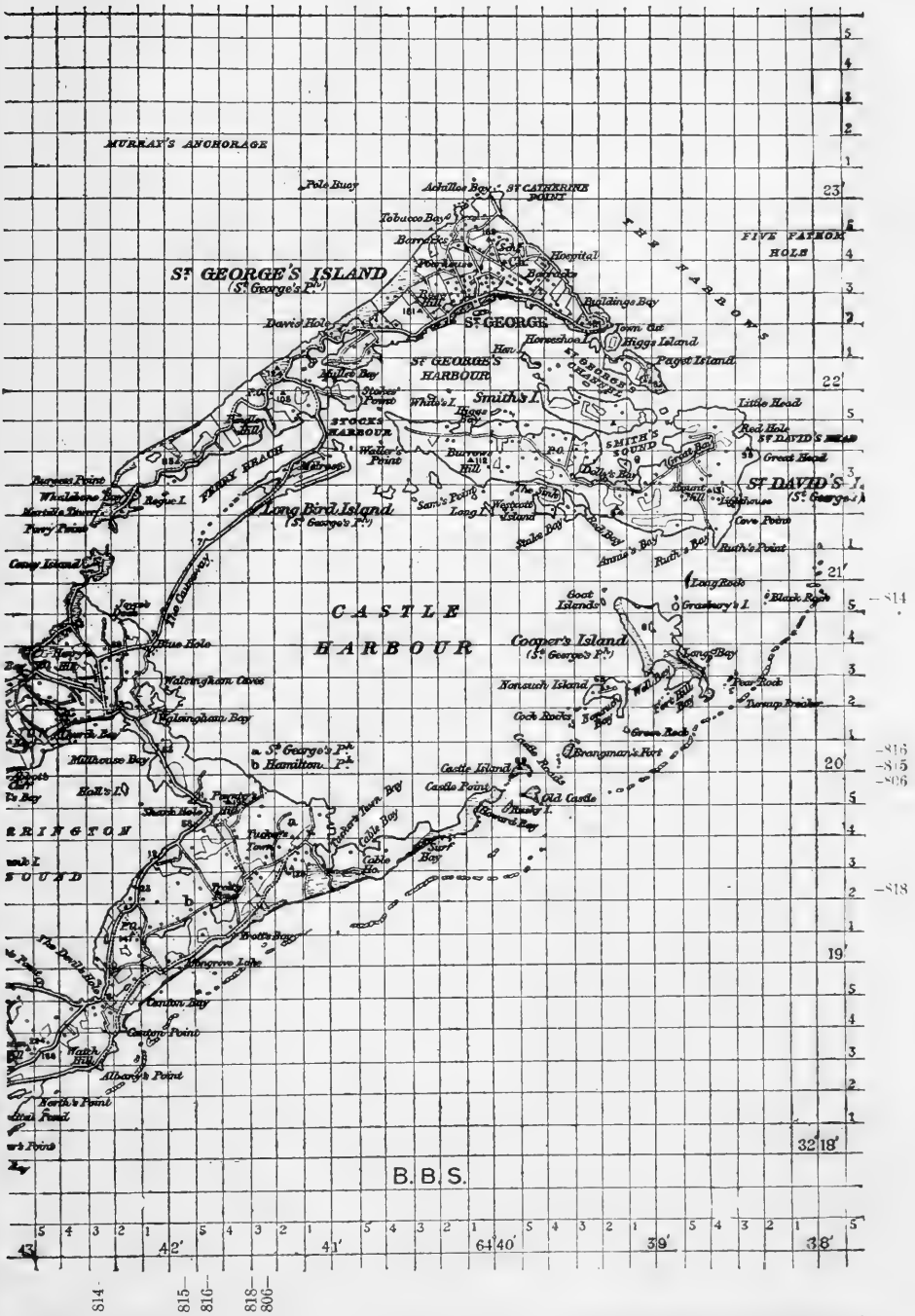
If this species were indigenous we could expect it to be as abundant formerly as it is now. Instead of that it seems to be entirely absent from the beds I examined. The evidence seems to me strong that its real home is elsewhere.

Map 1.



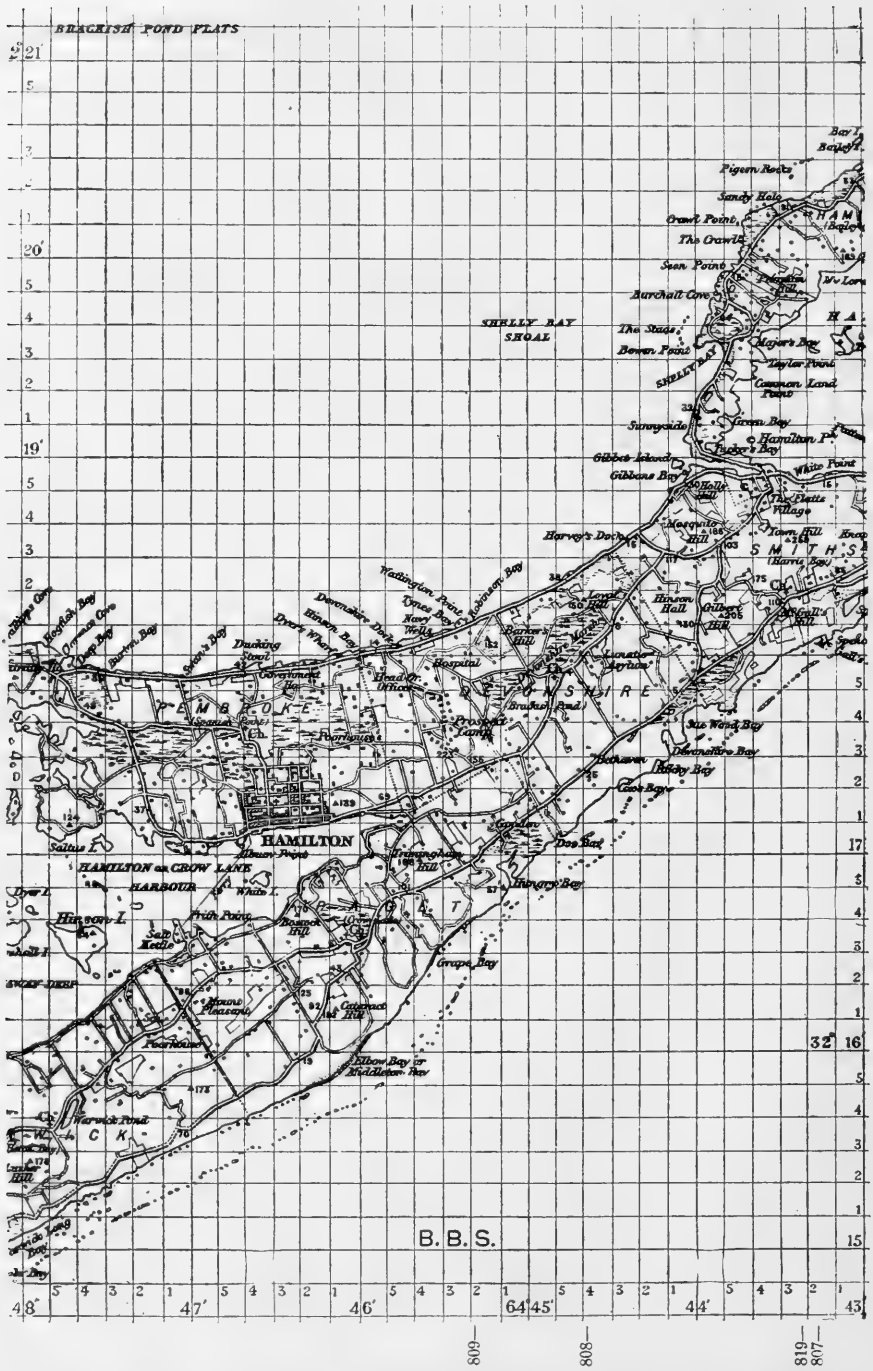
Bermuda Island.

Map 2.



Map of a part of Bermuda, with marginal indications of the latitude and longitude of collecting stations.

Map 3.



Map of a part of Bermuda, with marginal indications of the latitude and longitude of collecting stations.

Reference to Plate XXXVI.

Figures 2 to 5 are natural size; the others are variously enlarged.

Plate XXXVI Fig. 1.—*Pœcilozonites dalli.*
Fig. 2.—*Pœcilozonites cupula.* Locality 806.
Fig. 3.—*Pœcilozonites bermudensis zonatus.* Locality 808.
Fig. 4.—*Pœcilozonites nelsoni* form *discoides.* Locality 806.
Fig. 5.—*Pœcilozonites nelsoni callosus.* Locality 818.
Fig. 6.—*Vertigo numellata.* Locality 806.
Fig. 7.—*Vertigo marki.* Locality 806.
Fig. 8.—*Euconulus turbinatus.* Section from compact rock, locality 814.
Fig. 9.—*Euconulus turbinatus.* Locality 806.
Fig. 10.—*Euconulus turbinatus.* Locality 808.
Figs. 11, 12.—*Carychium bermudense.* Locality 806.
Fig. 13.—*Zonitoides bristoli.* Locality 818.

April 19.

The President, Samuel G. Dixon, M.D., in the Chair.

Seventy-six persons present.

The deaths of Edwin Sheppard, April 7, and E. W. Clark, April 9, members, were announced.

The Publication Committee reported that papers under the following titles had been offered for publication:

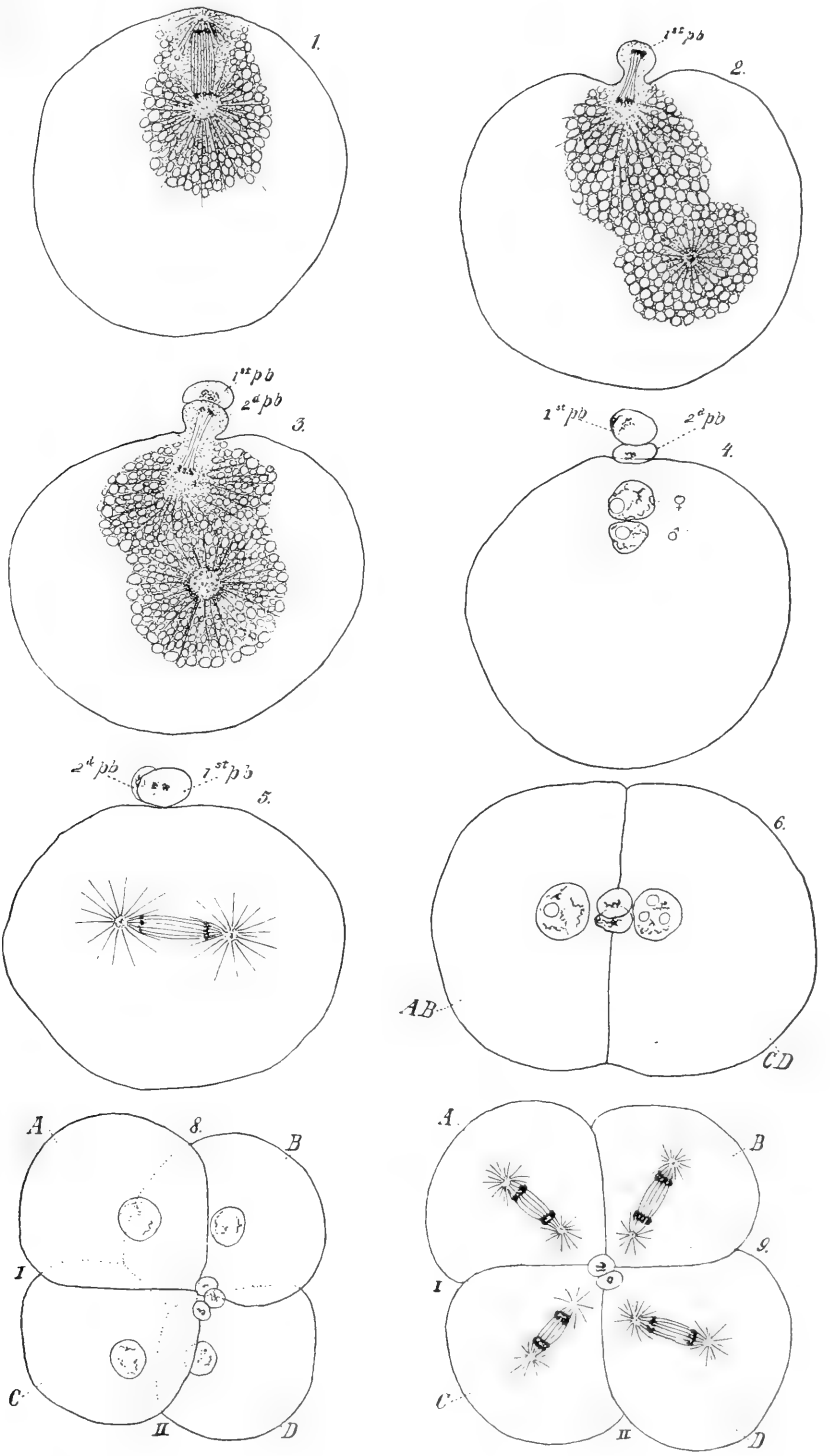
"A Monograph of the Genus Dendrocincla Gray," by Harry C. Oberholser (April 8).

"Post-Glacial Nearctic Centers of Dispersal for Reptiles," by Arthur Erwin Brown (April 11).

Dr. E. G. Conklin made an illustrated communication on the earliest differentiations of the egg, with special reference to the mechanism of heredity and evolution. (No abstract.)

The following were elected members: Everett F. Phillips, Herbert Guy Kribs, Henry R. M. Landis, M.D.

The following were ordered to be printed:



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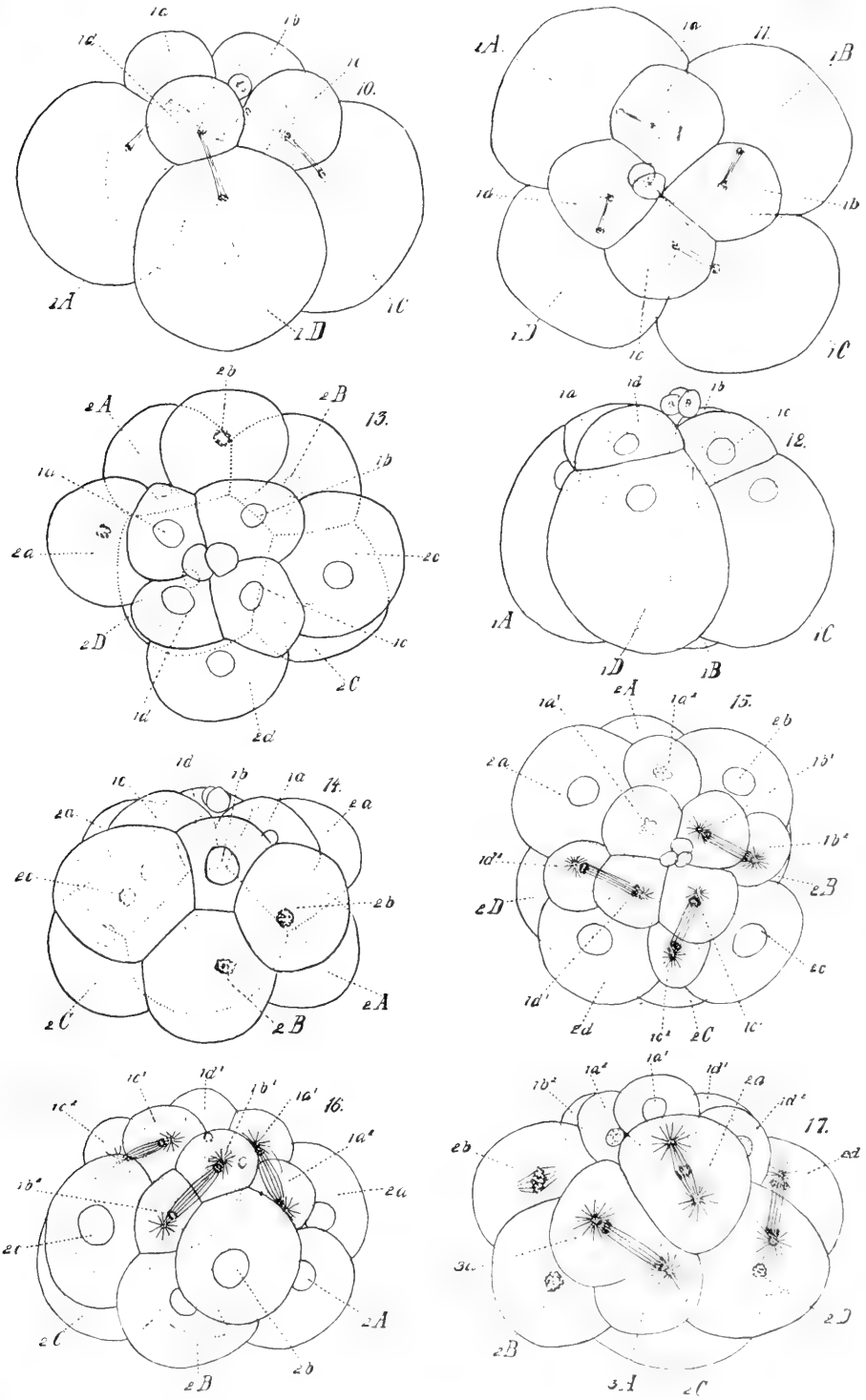

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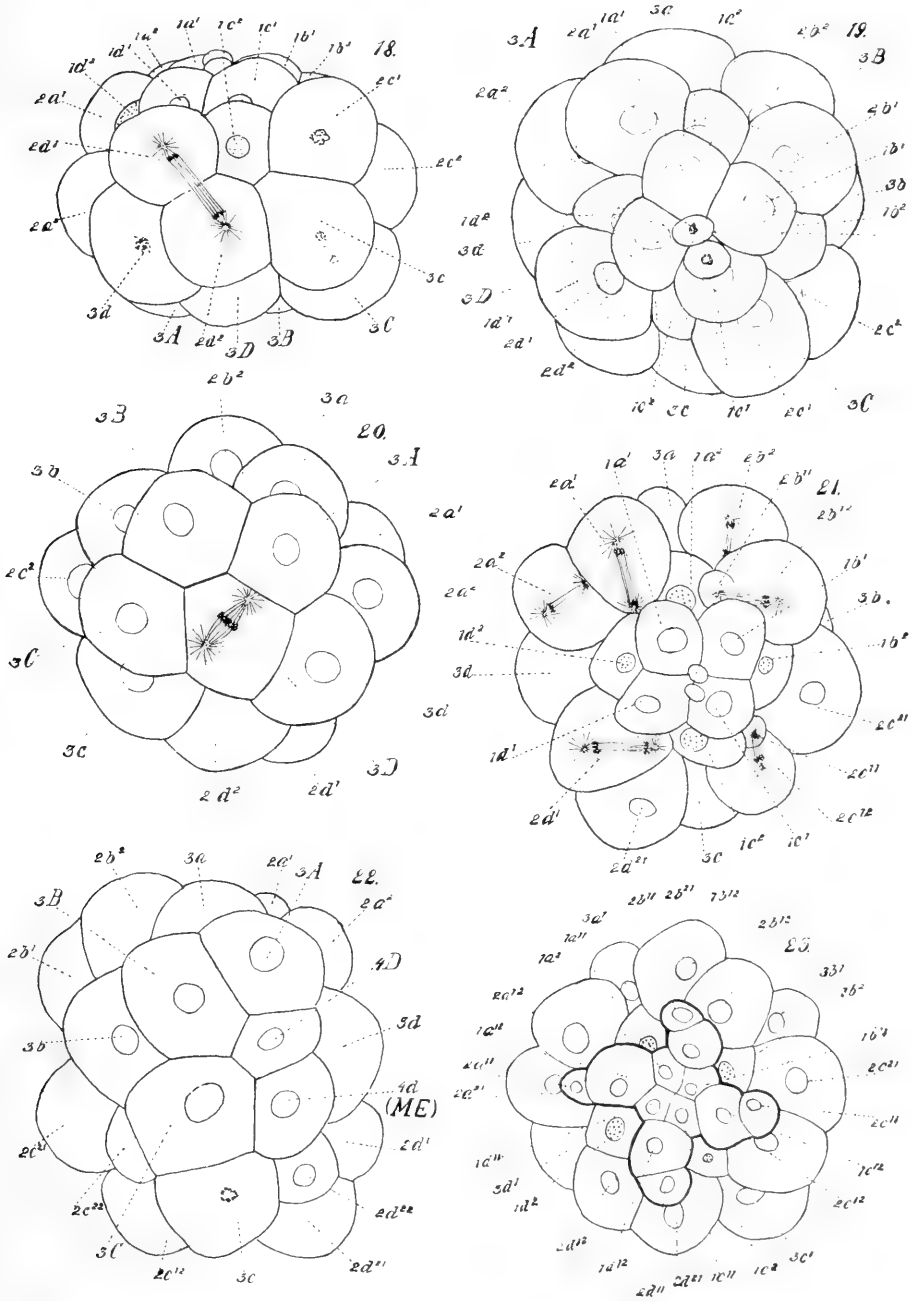

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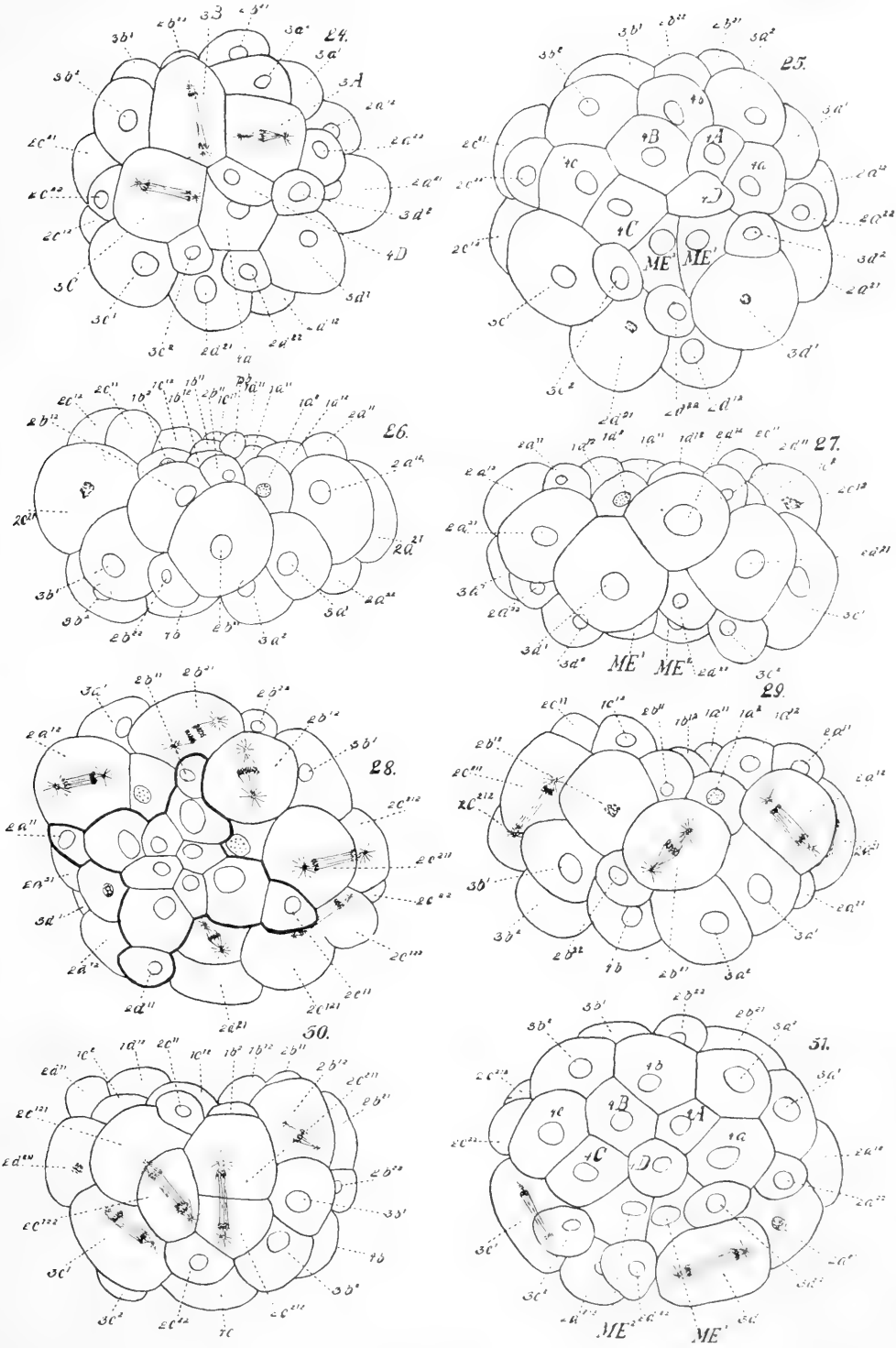
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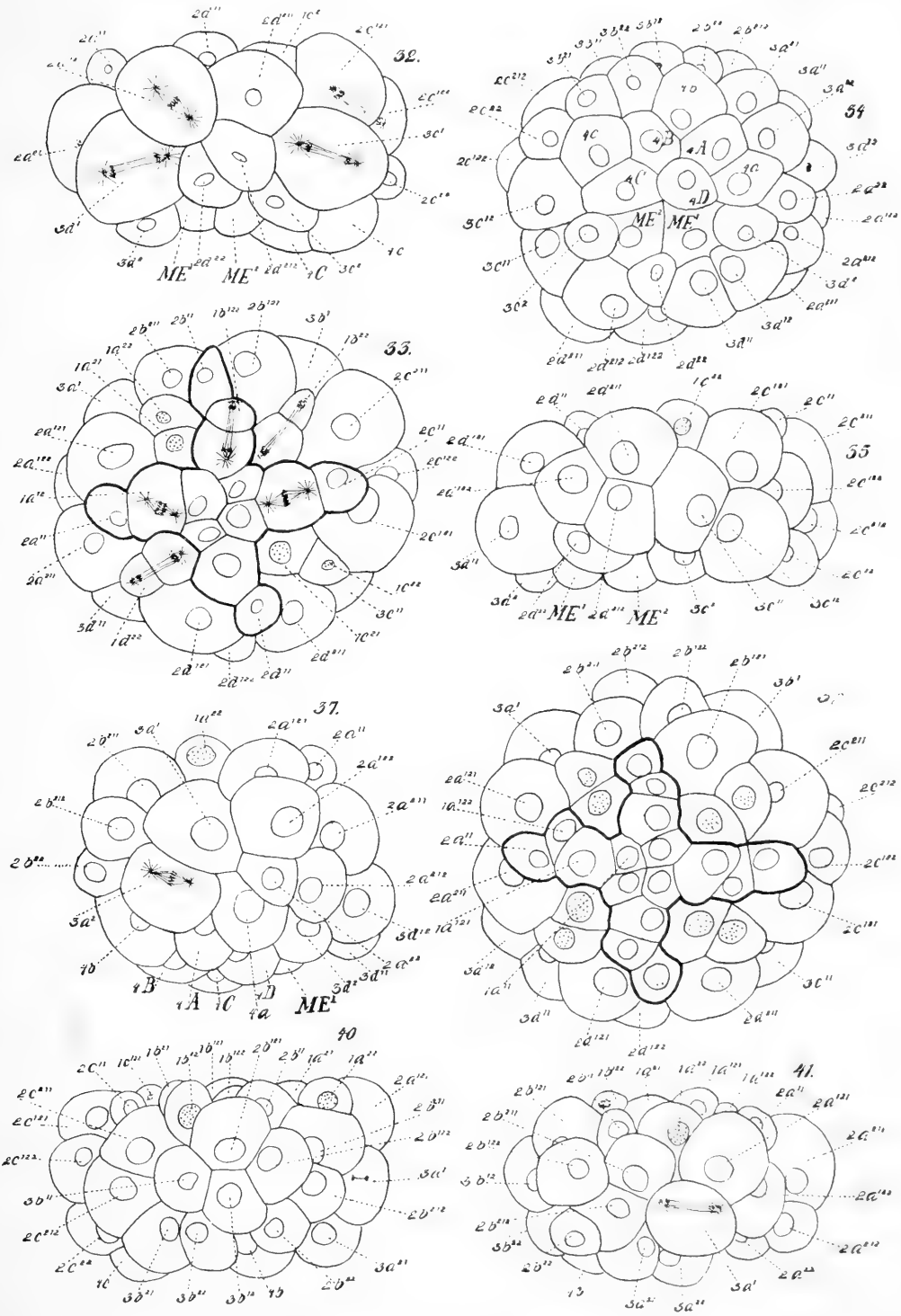

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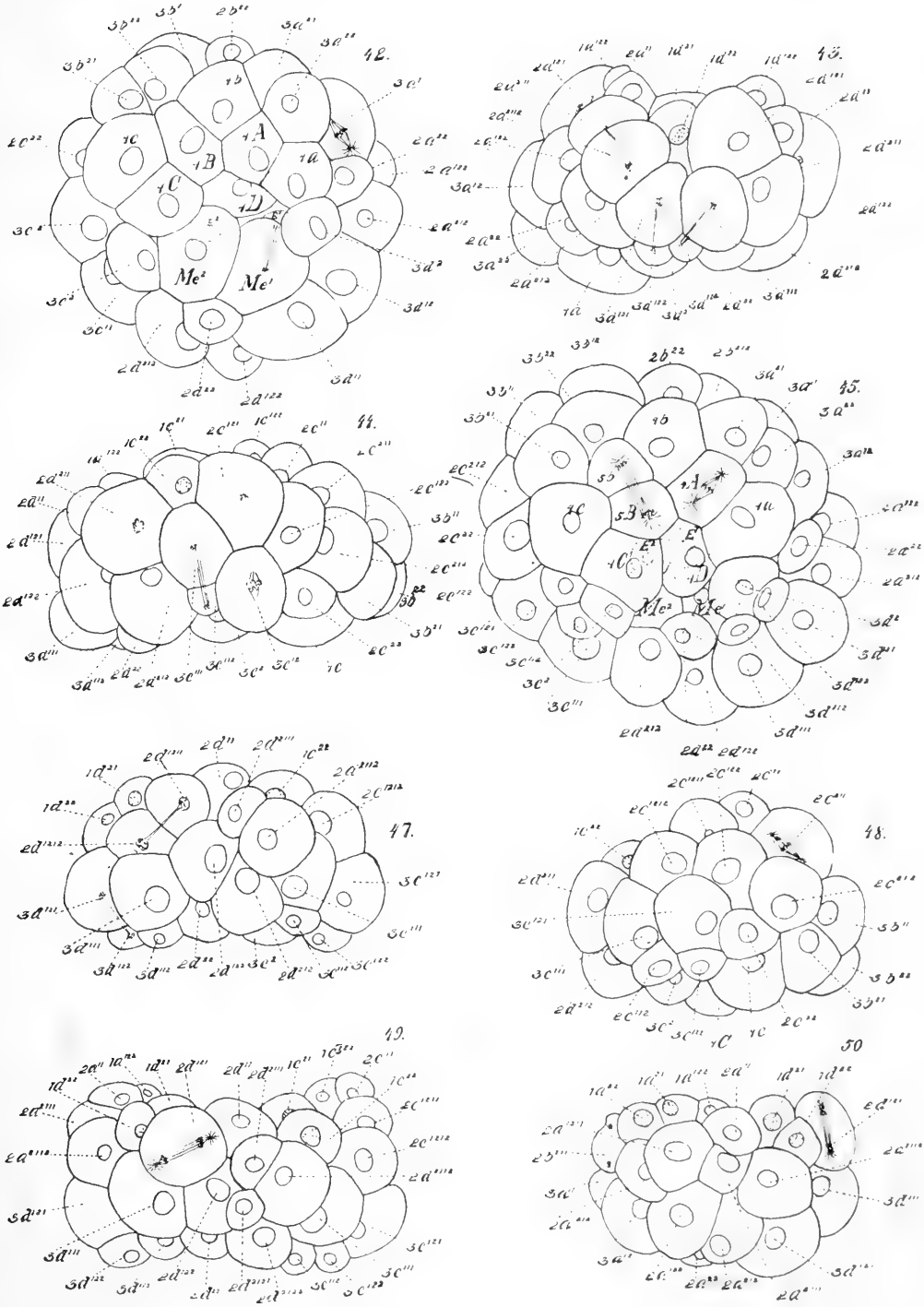

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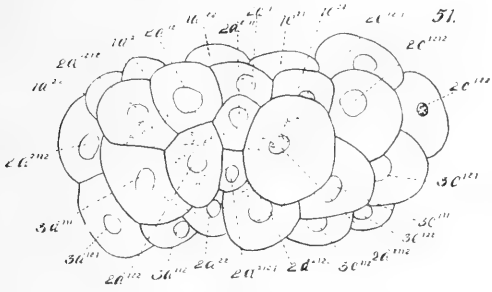

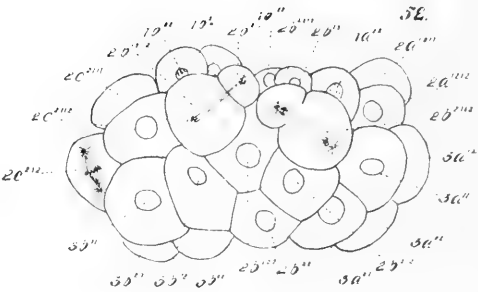

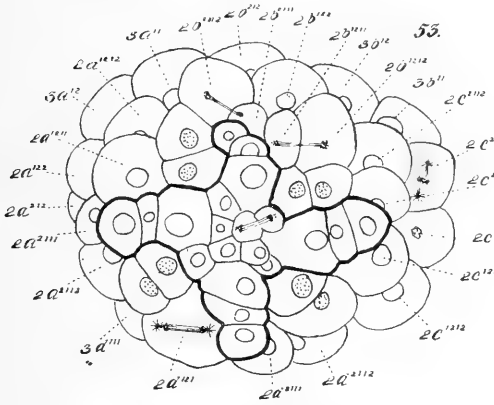

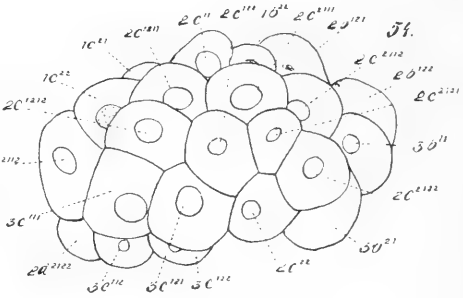

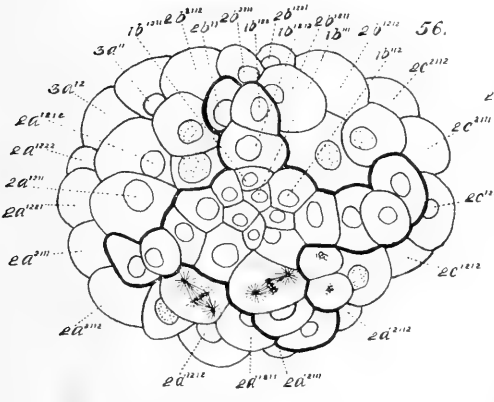

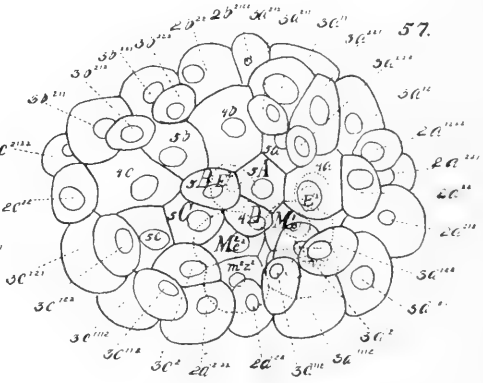

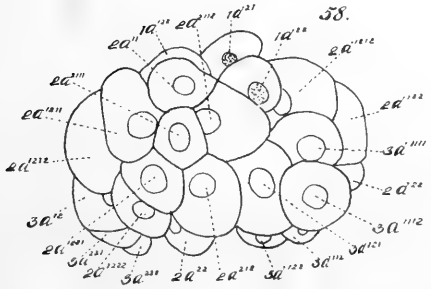

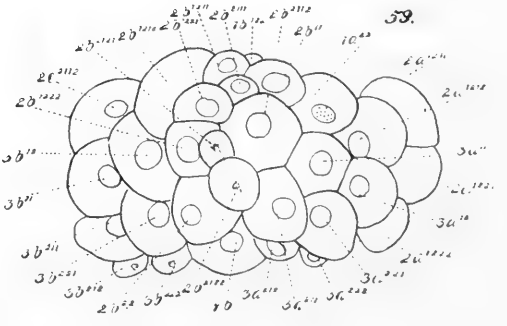

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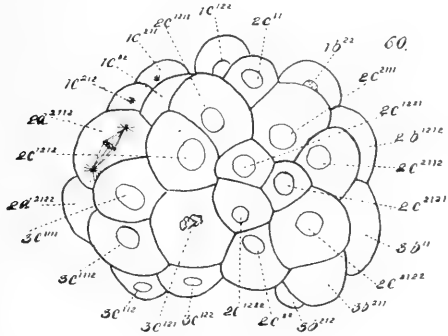

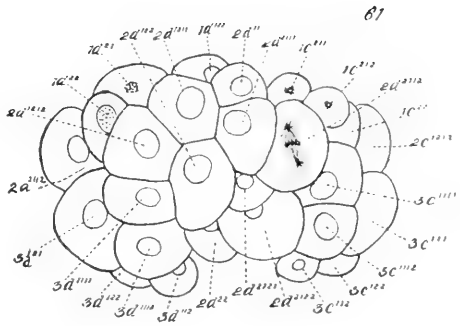

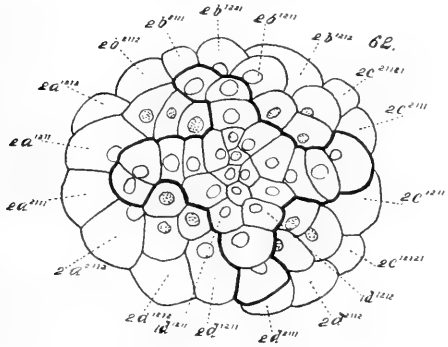

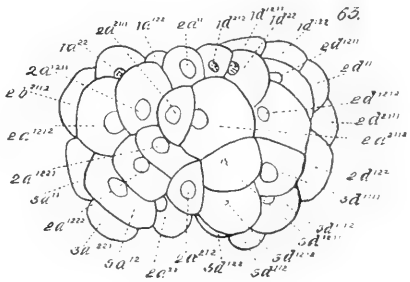

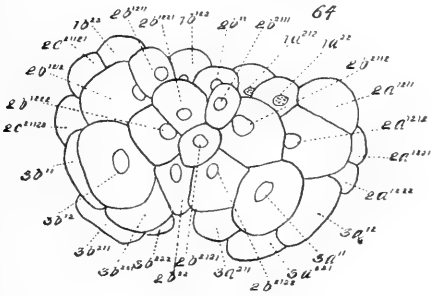

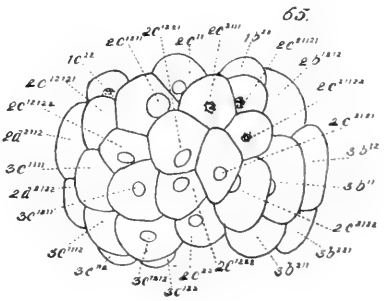

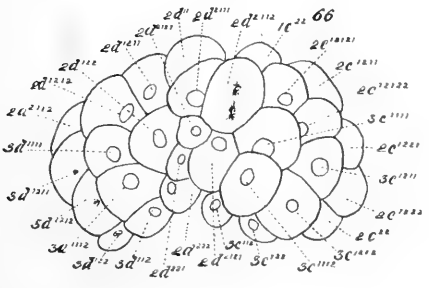

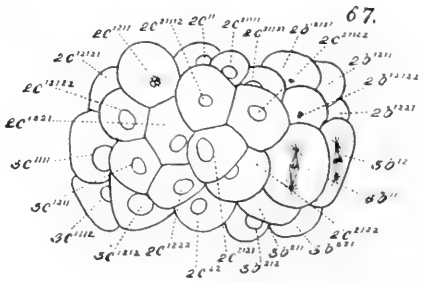

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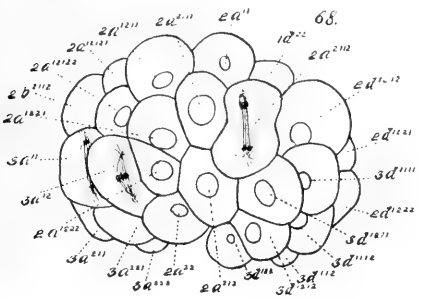

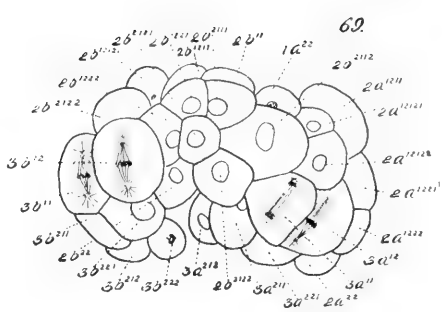

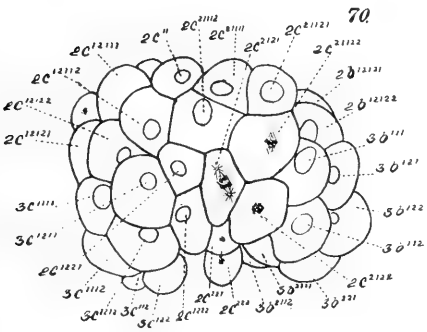

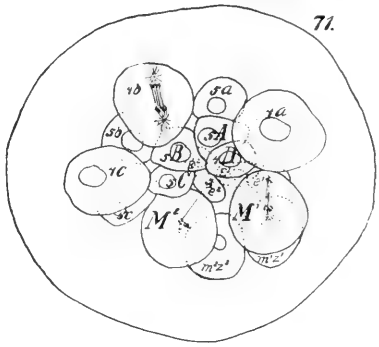

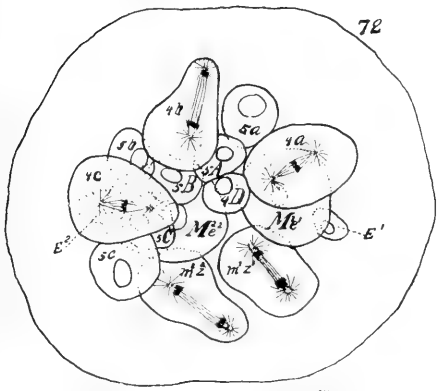

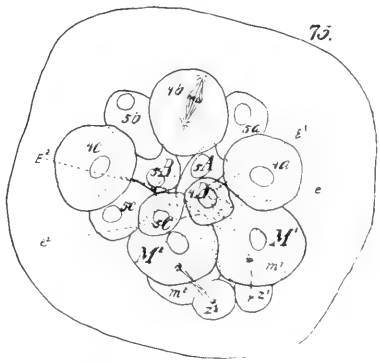

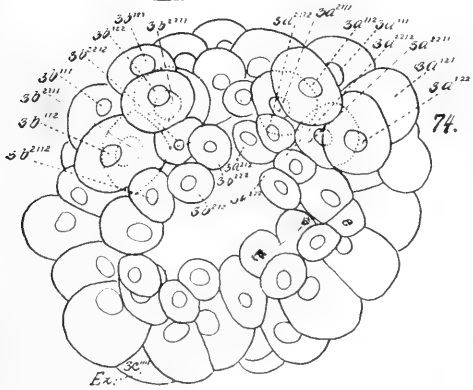

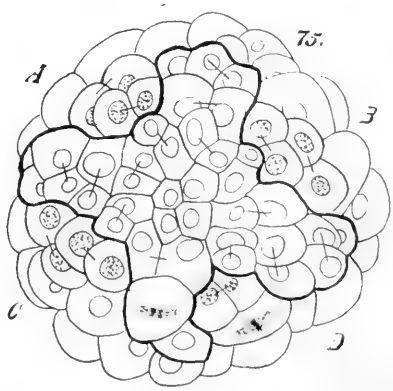

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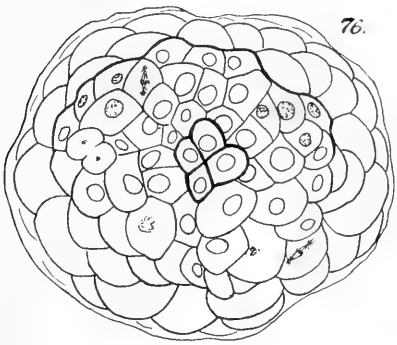

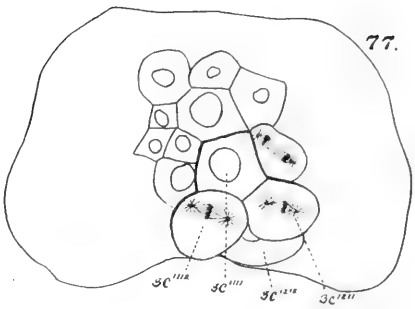

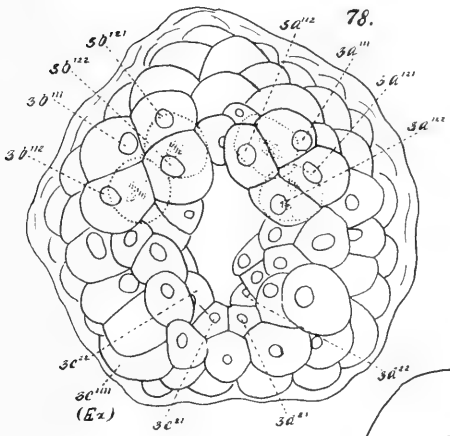

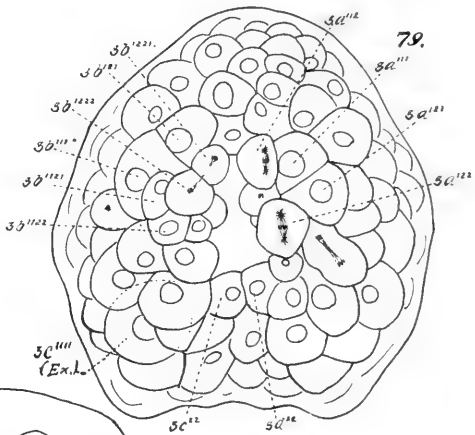

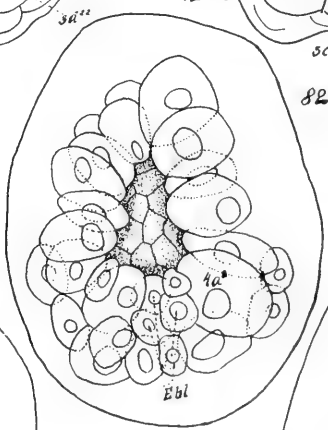

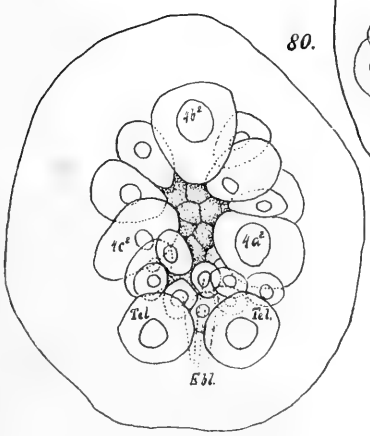

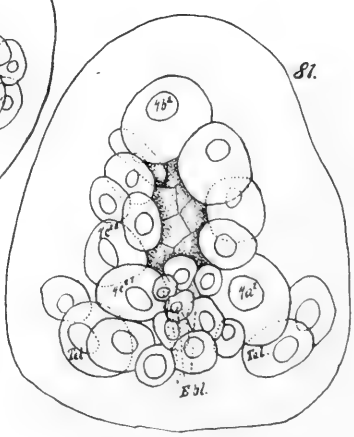

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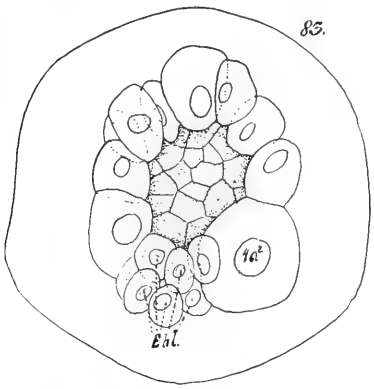

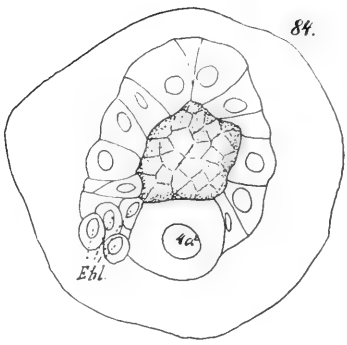

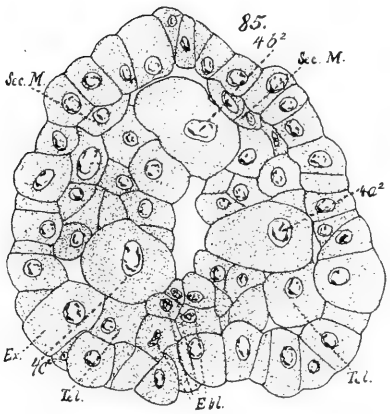

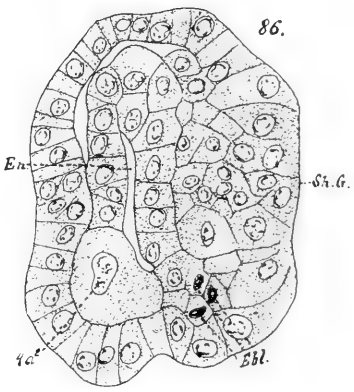

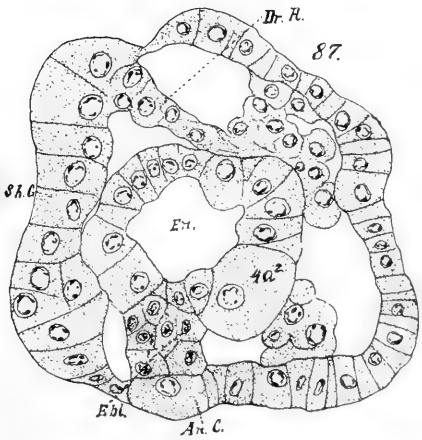

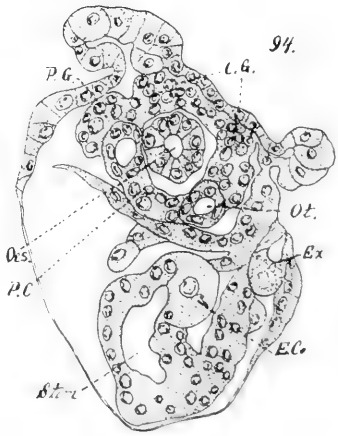

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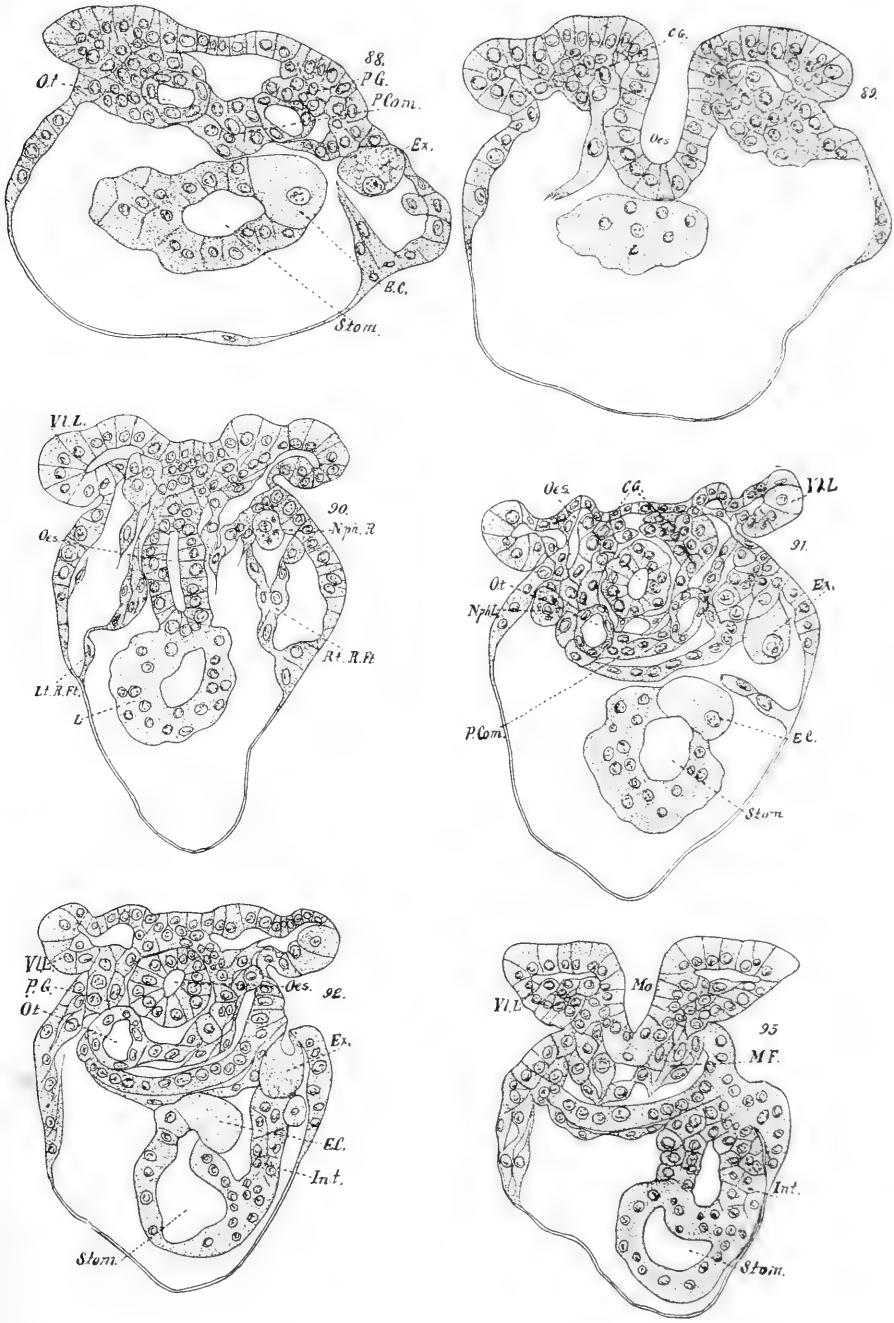

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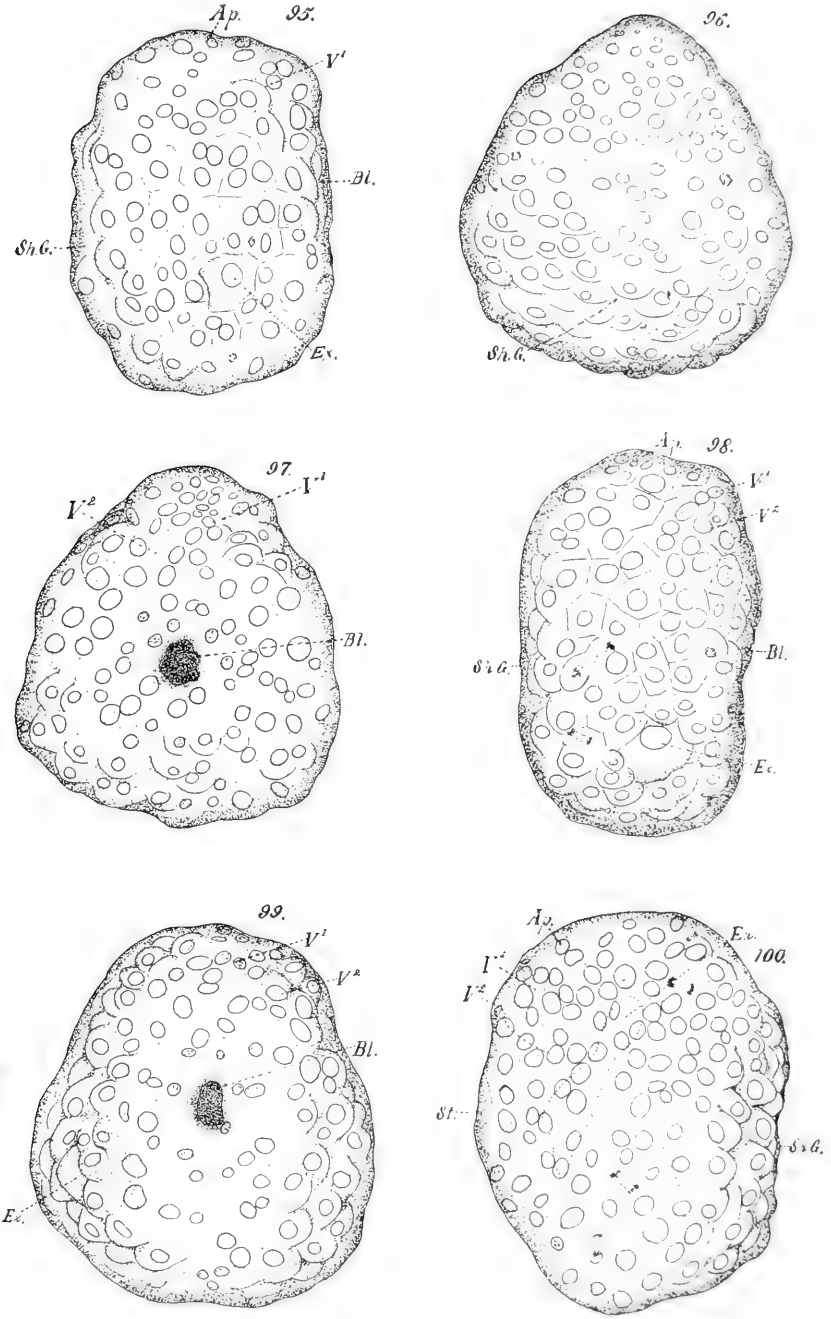

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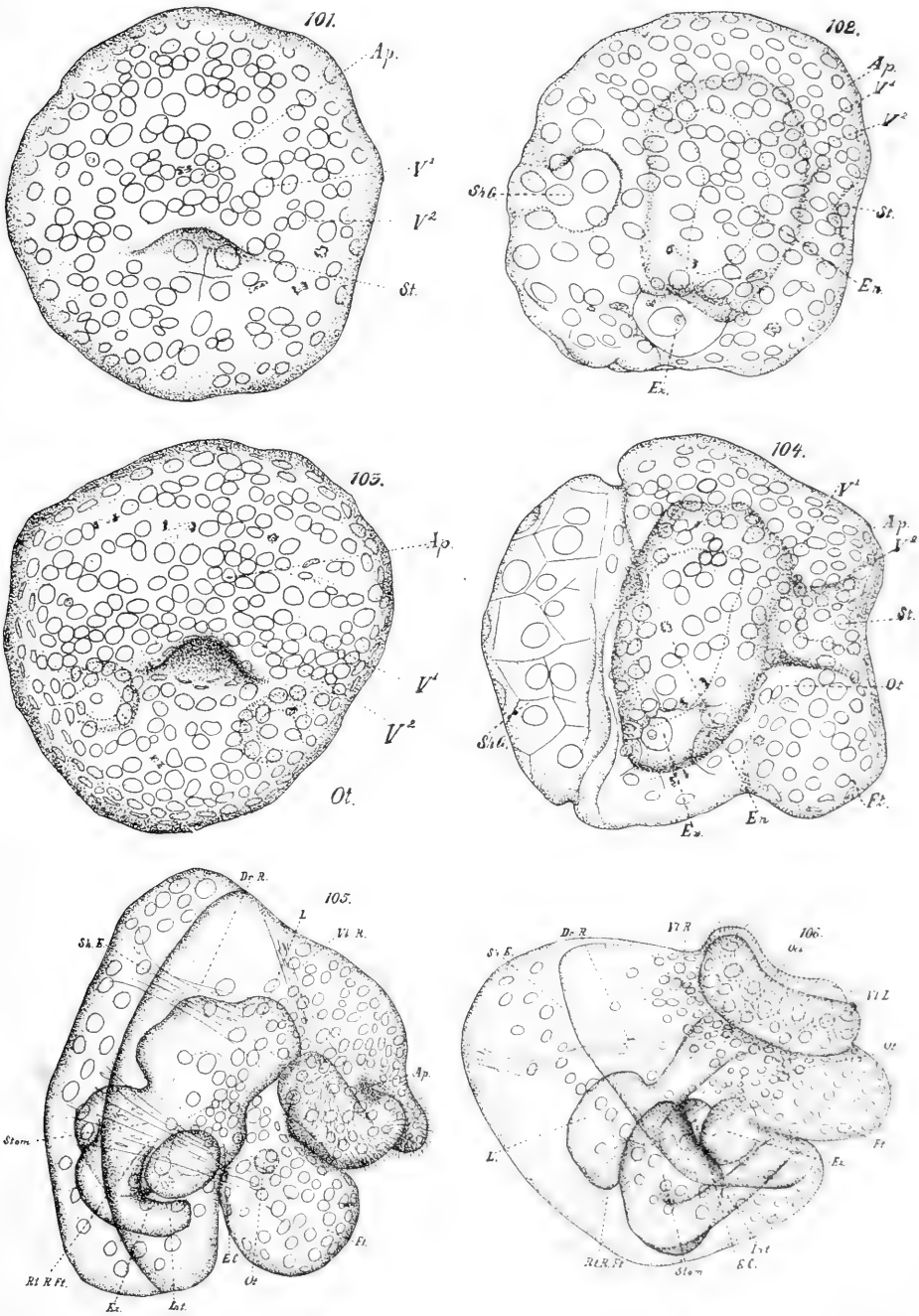

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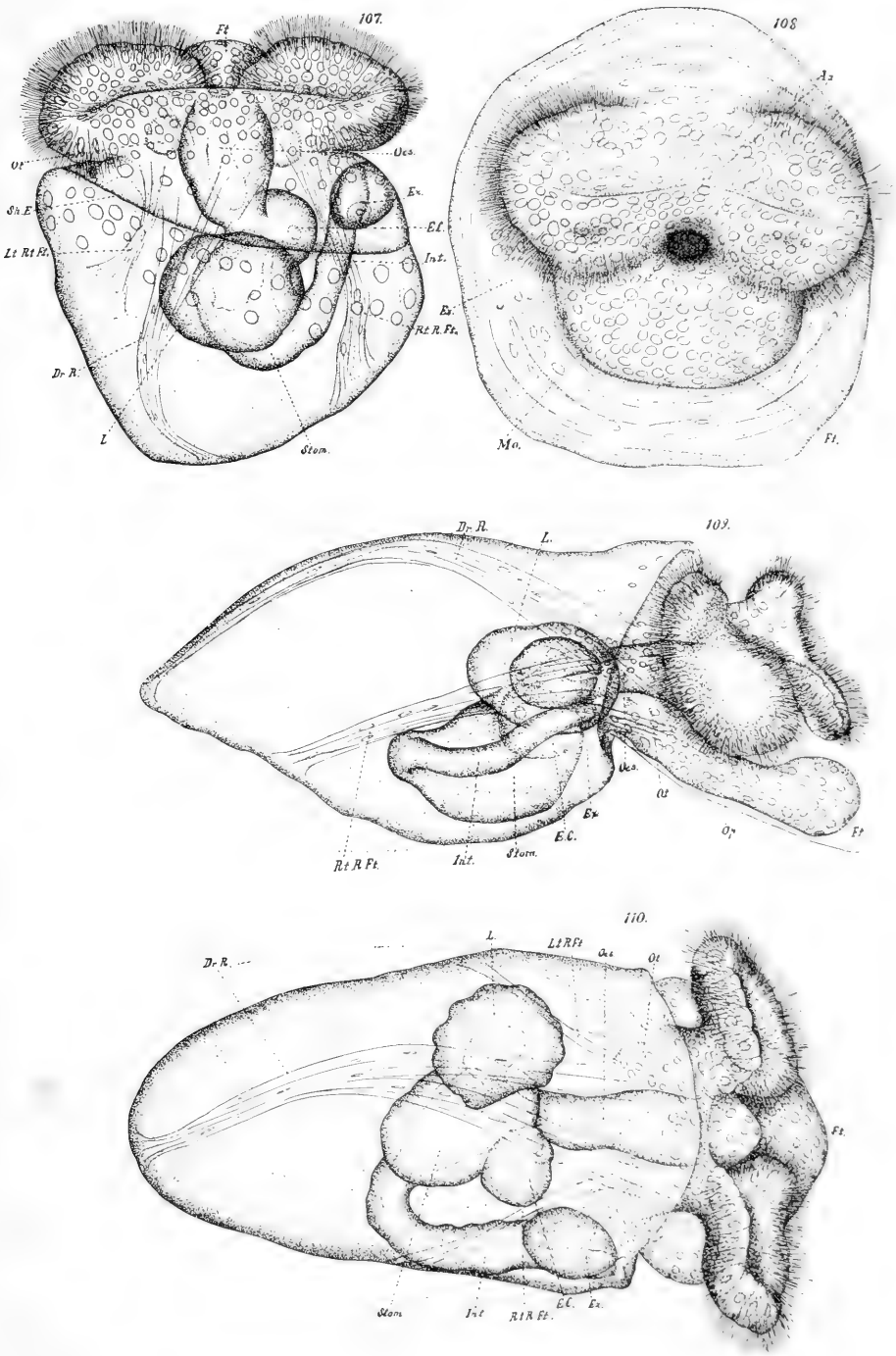

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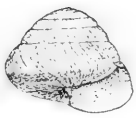

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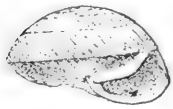

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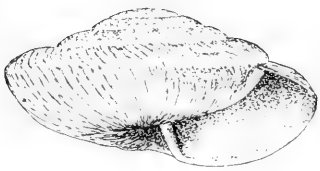

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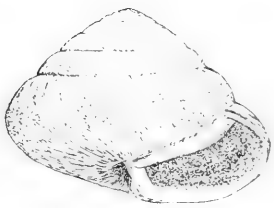

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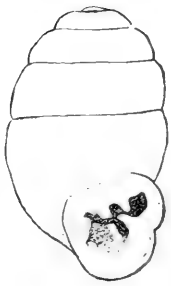

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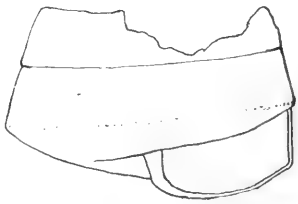

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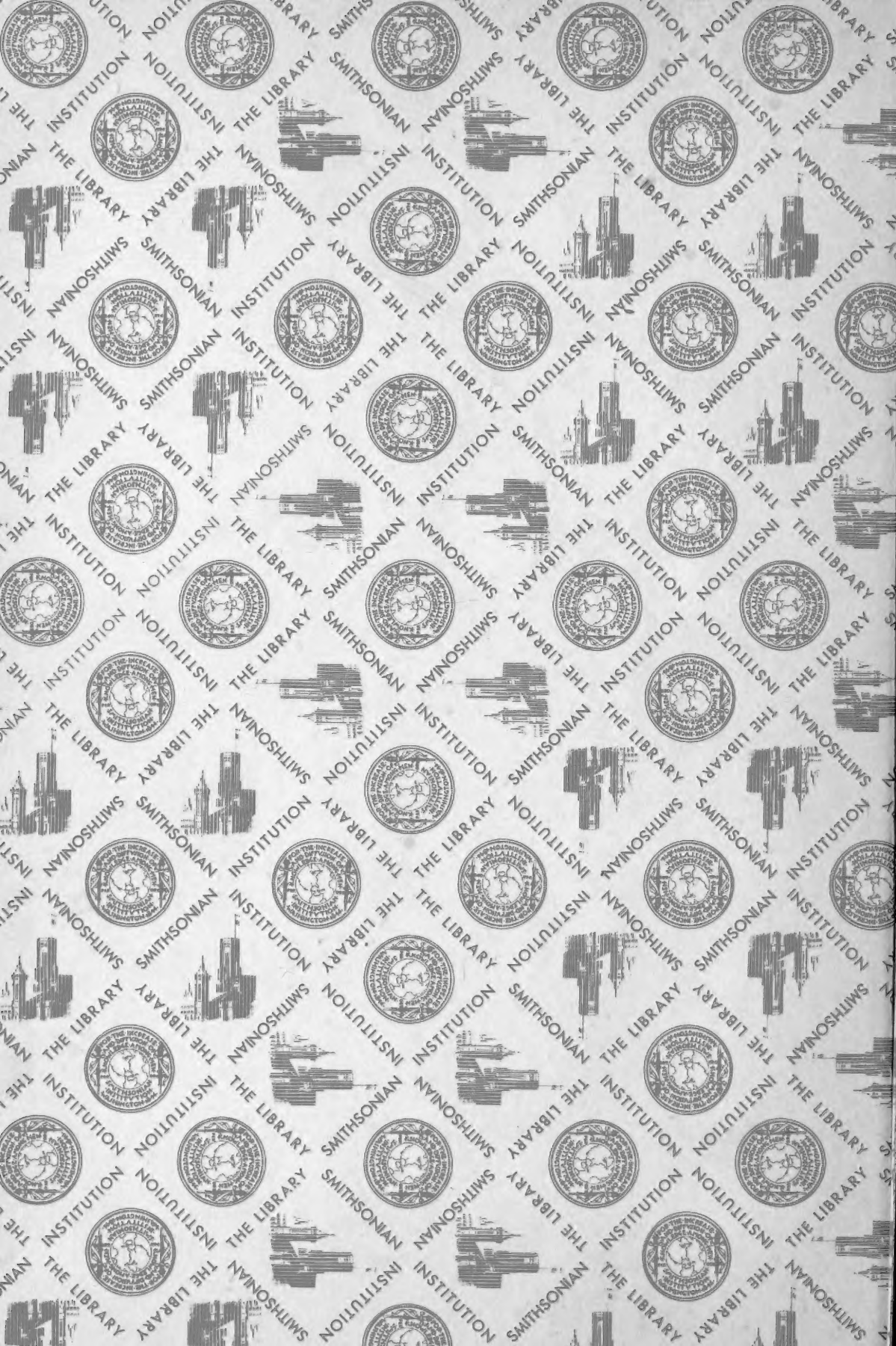
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